Feeding Patch Selection of African Buffalo (*Syncerus caffer caffer*) in the Central Region of the Kruger National Park

by

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Declaration of own work

I hereby declare that the dissertation submitted for the degree M Tech: Nature Conservation, at Tshwane University of Technology, is my own original work and has not previously been submitted to any other institution of higher education. I further declare that all sources cited or quoted are indicated and acknowledged by means of a comprehensive list of references.

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Abstract

Buffalo feeding patch selection was investigated using several methods. A phytosociological classificatory approach was used to describe the structural and floristic composition of feeding and control patches. The key differences between the two treatments were that feeding patches had a higher abundance of preferred forage species, higher grass biomass and cover, with a lower woody cover when compared with control patches.

Statistical analyses revealed that grass abundance was significantly higher in feeding patches, and that the valley bottom geomorphological unit was selected significantly more than other units. Distance to surface water was also significantly nearer to feeding sites than control counterparts.

Canonical ordination also revealed that feeding patches contained higher abundances of preferred forage species than did control patches. This factor as well as grass biomass, maximum visibility, distance to water and percentage leaf Phosphorus are important variables in patch selection.

Insight gained from this study suggests that buffalo patch selection cannot be attributed to a single patch variable, but instead is determined by a set of variables.

Grass species that were dominant in feeding patches as well as being highly favoured forage species include, *Panicum maximum, Urochloa mosambicensis, Digitaria eriantha, Themeda triandra, Heteropogon contortus* and *Panicum coloratum.*

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1 Chapter 1: General introduction

Selection of suitable habitats by free-ranging animals is mediated by a number of fundamental requirements, including suitable forage, proximity to drinking water, predator avoidance and protection from environmental extremes (Sinclair, 1977). These factors may not be mutually exclusive and an animal may try and optimise by choosing habitats that offer the greatest combinations of its key resources. Sinclair (1977) found that buffalo in East Africa showed regular or seasonal movement, associated with the occupation of different habitats at different times of the year. These movements reflect adjustments in meeting resource requirements, especially fluctuations in the availability of food and water. Buffalo foraging behaviour and habitat selection is well documented (Sinclair, 1977; Beekman & Prins, 1989; Funston, 1992; Prins, 1996). Most of these studies are only of local use though, as vegetation types, landscape characteristics and climate vary significantly from one study area to another. Senft *et al.* (1987), McNaughton (1991) and Bailey *et al.* (1996), suggested that large herbivore grazing distribution patterns are hierarchical in nature, and thus animals have varying scales of diet selection. Broadly stated, selection begins at a small scale (cartographically speaking) or landscape level, progressively getting to a finer scale through the feeding patch, feeding station or micropatch and finally, plant part or bite. Three studies (Mugangu *et al.*, 1995; Perrin & Brereton-Stiles, 1999; Abeare, 2004) have described the patch characteristics of herds, depicting their selection of preferred feeding sites within the mosaic of the landscape.

In this study, I quantify the patch selection of buffalo within the Kruger National Park (KNP), supplying insight into the patch selection criteria of mixed-sex buffalo herds within the KNP system.

The fieldwork was carried out in the central region of the KNP from February 2002 until July 2003.

The objectives and key questions of the project were as follows:

<u>Objective 1:</u> To describe buffalo feeding patch floristic characteristics and determine whether a difference in floristic composition exists between feeding patches and a neighbouring control site.

Objective 2: To compare the habitat characteristics of the patches selected by buffalo to that of a neighbouring control site.

Key questions:

2.1.) Which measured variables show a significant difference between feeding and control sites?

Thus to determine whether selection for the measured variables takes place at the set sampling scale or are certain variables being selected at a different scale?

2.2.) Does predator avoidance have an influence on patch selection?

Objective 3: To determine how floristic composition and structure interact with environmental variables to determine patch selection.

Objective 4: To quantify and describe forage selection of buffalo and how grass attributes may influence this selection.

Key questions:

4.2.) Do moisture content, nitrogen and phosphorus content and stem to leaf ratios influence the selection of those grass species.

Objective 5: Interpret the data from this study and make recommendations as to the sustainable management of buffalo.

These objectives collaboratively aim to ascertain if common habitat preferences exist between mixed sex herds across different substrates and to quantify buffalo utilisation and prioritisation of seasonal resources.

1.1 Previous studies conducted on the feeding ecology of the African buffalo within the region

To place this work in context, cognisance must be taken of several other feeding-related studies that have been carried out in the KNP. A brief review and comparison is made with my research.

Abeare (2004) used buffalo herd dry-season locational data to test the effectiveness of the new home range estimator, k nearest-neighbour convex-hull (k-NNCH) developed by Getz and Wilmers (2004). Similar methodology was employed in the vegetation sampling for this study, namely an adapted version of the Plant Number Scale (Westfall and Panagos, 1988), to differentiate floristically, high-use and low-use areas at two sampling scales, habitat-level and patch-level. The adaptation involved only identifying the graminoids to species level, while all woody plants where placed into one category, with no differentiation of species. At the landscape level, nine out of the ten region-wide vegetation types as identified by Gertenbach (1983) were represented. Buffalo showed a significant selection for dwarf knob thorn savanna and knob thorn/marula tree savanna vegetation types (Gertenbach, 1983).

The patch selection analyses revealed a significant difference in river density between core-use and lacunae (low-use) patches and the abundance of certain grass species classes (moderately palatable).

Abeare's analyses of grass preference indices illustrates that the abundance of the most-preferred species varies little between substrates and patch treatments, whereas for less preferred species greater abundances are found within core-use patches.

The results of this patch analysis differs somewhat from my results whereby the relevant abundance of preferred species is higher in feeding patches than in neighbouring control patches.

Macandza *et al.* (2004) conducted research into the late dry season forage selection of buffalo across the two dominant geological substrates. The sampling was conducted at the feeding station level to monitor species selection of the herds over the late dry season or so-called "crunch period", when resources are most limited, and to test foraging theory which predicts an increase in the dietary composition of previously avoided species as the dry season progresses. The forage selection findings of this study concur strongly with my findings.

Wentzel *et al*. (1991) characterised the herbaceous layer of preferred grazing areas of grazers in the south-eastern KNP, including buffalo. Their results showed that buffalo selected areas with a higher percentage of Decreaser classified grasses in the sward than did the other species under investigation; and that buffalo selected areas with a better overall veld condition. Among these Decreasers were *Cenchrus ciliaris, Digitaria eriantha, Panicum coloratum, Panicum maximum, Themeda triandra* and *Setaria incrassata*, all species shown in my research to rank amongst those preferred by buffalo. Buffalo also selected areas of a higher phytomass.

Pienaar (1969) provide cursory data on grass species found in the rumen of culled buffalo. Preliminary results showed *Themeda triandra, Panicum coloratum, Digitaria* sp., *Panicum maximum* and *Heteropogon contortus* to be abundant in their diet. These results imply that buffalo forage selection remains consistent both spatially and temporally with the KNP system.

This study differs from previous studies in that a combination of methods was used, including phytosociology, pair-wise and canonical ordination, providing a holistic overview of feeding patches and their selection criteria.

1.2 Study Area

1.2.1 Location

The study was conducted in the central region of the Kruger National Park (Figure 1), the core area of the study being in the vicinity of Satara rest camp (24°23'42S, 31°47'06E). The camp is situated at approximately 275m above mean sea level (a.m.s.l.).

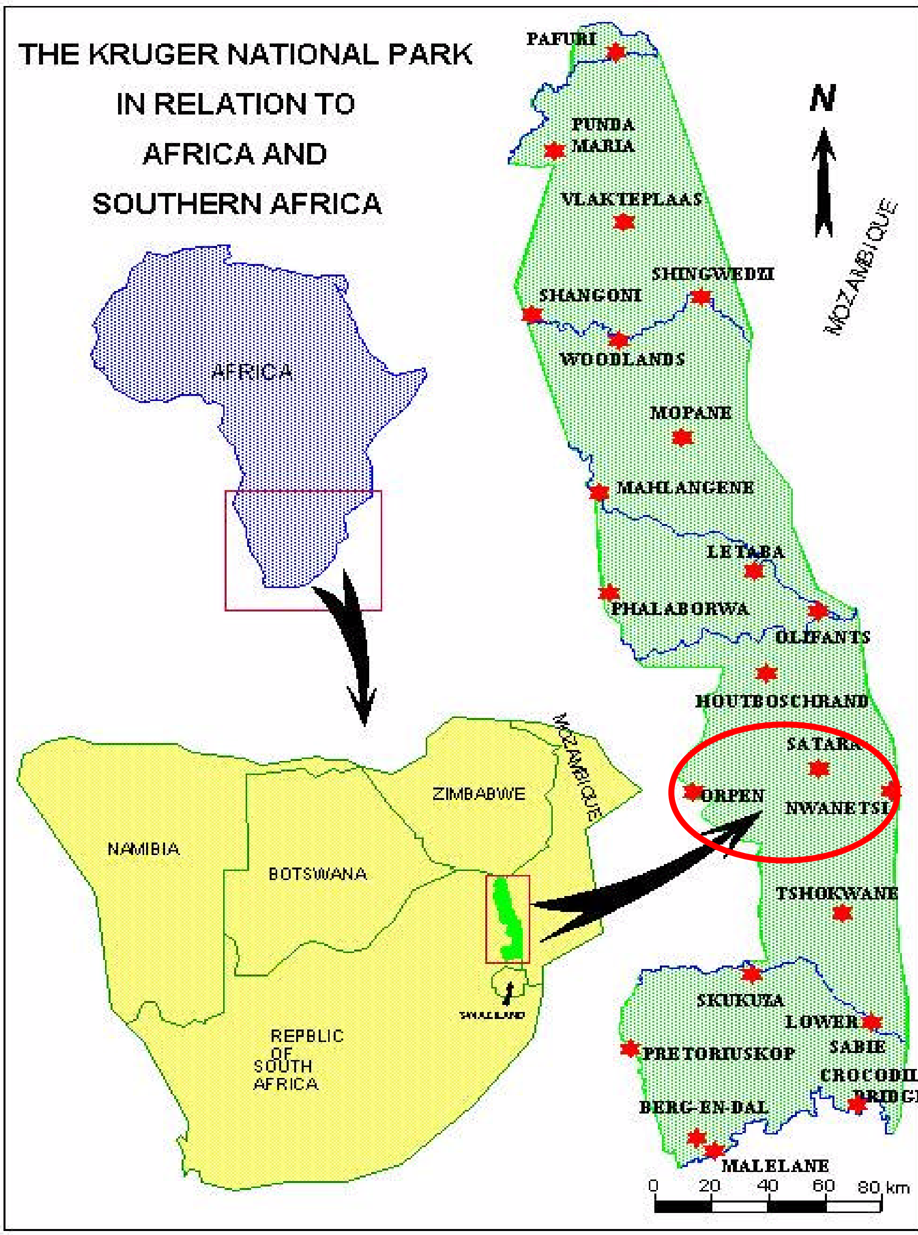


Figure1: Map showing study area at a continental, regional and local scale respectively (KNP GIS lab).

1.2.2 Climate

Climatic conditions in the KNP vary from hot and humid in summer to mild and predominantly dry in winter. The lowveld's climate is related to the regional climate of the sub-continent as a whole in that it is influenced by anticyclonic systems moving semi-rhythmically over Southern Africa from west to east (Venter & Gertenbach, 1986).

The average long-term rainfall for the study area can be seen in Figure 2.

Two seasons, wet and dry, were used for purposes of this study, based on the long-term monthly rainfall. They were classified as follows:

1) Wet season: November to April
2) Dry season: May to October.

1.2.2.1 Rainfall

The long-term average annual rainfall for the Satara region is 550mm (Gertenbach, 1980).

Rainfall is largely confined to the summer months in the study area with very little to no rain experienced over winter (Figure 2). December, January and February are on average the wettest months of the year, while July and August are the driest (Gertenbach, 1980).

During the study period the central region of the park had well below average rainfall, with the only substantial rain occurring in one event in March 2003.

Rainfall in the KNP exhibits a cyclic nature with periods of above and below the long-term average rainfall occurring at regular intervals of approximately 9-10 years producing a *quasi* 20-year oscillation (Gertenbach, 1980). On average the precipitation in wet and dry cycles was 13% above and below the KNP long-term average. Annual precipitation within the park follows a gradient, decreasing in quantity from south to north (with the exception of the area around Punda Maria camp).

1.2.2.2 Ambient temperature

Ambient temperature for the entire KNP is tropical in nature, with extremely hot and humid summer conditions, and warm and dry winter conditions. The hottest temperatures are historically experienced over December and January, while the coolest months of the year are June and July (Figure 2).

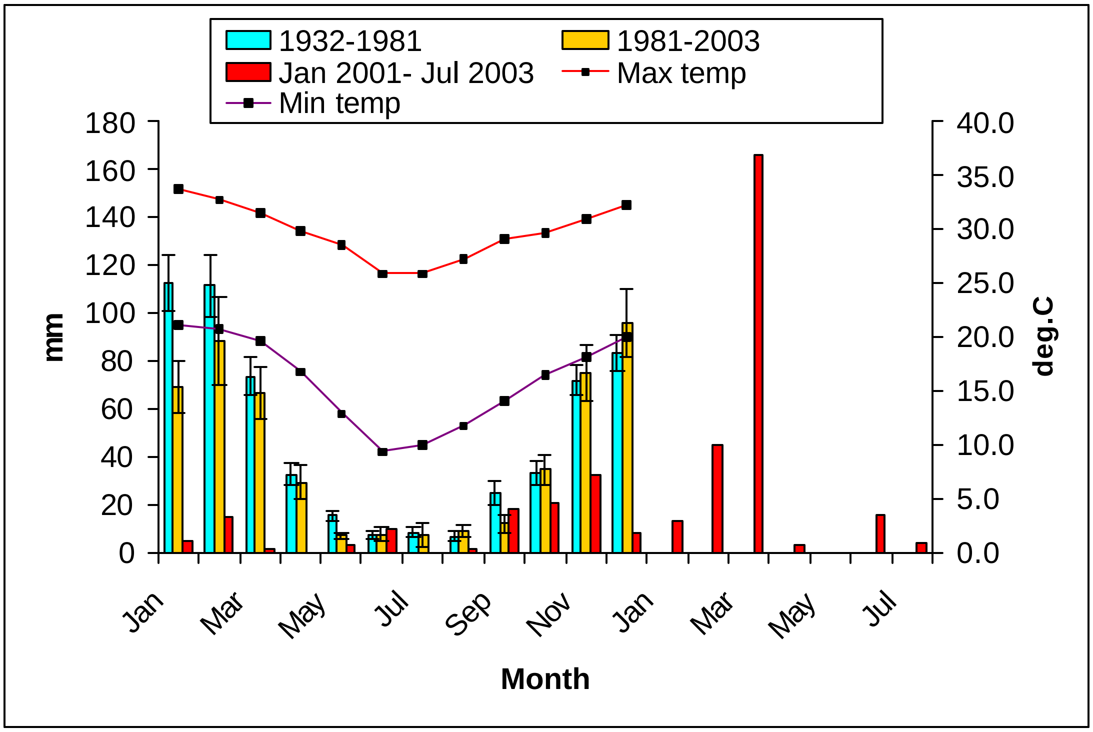


Figure 2: Mean long-term rainfall (1932-2003) as well as that for the study period (January 2002 – July 2003) for Satara (Data supplied by the South African Weather Bureau). Error bars represent 95% confidence intervals. Long-term minimum and maximum temperatures for Satara for the periods 1966-1971 and 1981-1990 are also displayed.

1.2.3 Geology, soils and geomorphology

The study area occurs predominantly in the Satara Land System (incorporating several Land Types) and is described by Venter (1990) as being associated with volcanic rocks of the Sabie river basalt formation, which consists mainly of olivine-poor lavas (Bristow, 1976; Bristow & Cleverly, 1983; Bristow & Venter, 1986), as well as gabbro of the Timbavati gabbro (Schutte, 1986) (Table 1). The Timbavati gabbro consists of quartz gabbro, gabbro and olivine gabbro and occurs as large plates which are intrusive in the Basement complex.

Table 1: Brief overview of the Land Type characteristics (Venter, 1990) of the study area.

L/TYPE	GEOLOGY	DOMINANT WOODY VEGETATION	GEOMORPHOLOGY
Mavumbye	Sabie river basalt formation with interlayers of olivine-rich basalt (picrite) of Letaba basalt formation.	Dense to open *A. nigrescens* bush savanna.	Flat-slightly undulating plains associated with interfluvial areas.
Muzandzeni	Orpen gneiss intruded in some places by numerous dolerite dykes.	Moderately dense mixed *Combretum* sp./*A. nigrescens* bush savanna.	Slightly-moderately undulating plains representing areas where erosional processes caused shallower soils.
Orpen	Timbavati gabbro (quartz gabbro, gabbro and olivine gabbro) occur as differentiated plates in Basement complex.	Isolated patches with moderately dense *C. apiculatum/C. zeyheri* bush savanna on granitic inliers.	Gently undulating plains.
Satara	Olivine-poor basalt of Sabie river basalt formation intruded by dolerite dykes.	*Acacia nigrescens/Sclerocarya birrea* tree savanna. *Dichrostachys cinerea* prominent shrub.	Flat-slightly undulating plains associated with interfluvial areas.
Vutome	Ecca shale/mudstone; Clarens sandstone/dolerite/basalt; Colluvium from sandstone/gneiss over shale/mudstone.	*A. welwitschii/E. divinorum* tree savanna with *Spirostachys africana* near drainage channels.	Flat-slightly undulating with scattered low koppies & rock outcrops.

2 Chapter 2: Description of buffalo feeding habitats

2.1 Introduction

Individuals, populations, and species of large herbivores are influenced by spatial heterogeneity in their environments at scales ranging from the feeding patch to the biome (du Toit, 2003). This chapter places feeding patches sharing similar vegetation structure and species composition collectively into community types or habitats. Phytosociology was used to describe the physiognomic-structural and floristic properties of the experimental and control patches. Phytosociology is the science of recognition and definition of different vegetation types and plant communities (Kent & Coker, 1996) involving the orderly arrangement of relevés (sample or patch) according to their differences and similarities (Gabriel & Talbot, 1984). The classification of feeding patches into plant communities allows for *inter alia* the assessment of vegetation types and their suitability as habitats for buffalo. One can then deduct buffalo feeding habitat preferences within the Kruger system and extrapolate these to other areas, geographically or floristically similar.

While the following description of buffalo habitats is of largely local significance, knowledge gained from these data may also be applied to any conservation area as it includes both the woody and herbaceous characteristics (including *inter alia*, density, canopy cover, phytomass and spacing) of the communities selected for by buffalo, irrespective of species composition. The key factors independent of species composition being:

- Woody density, across three growth form categories according to height of the plant after Westfall (1992):
  Tree (single stem >=2m, multi-stem >=5m)
  Shrub (single stem <2m, multi-stem <5m)
  Dwarf Shrub (<1m, perennial)
- Herbaceous phytomass, percentage canopy cover, plant spacing and density.

Hence, species composition may change geographically but the plant abundance indices can be used for buffalo ecology comparisons between different areas or populations. Grass species preferences shown for this study area can be extrapolated to other areas based on the palatability indices given for those preferred species (e.g. percentage Nitrogen and Phosphorus content and stem to leaf proportion).

Two vegetation classifications have been completed for the KNP to date:

- Venter (1990) conducted a comprehensive study to map and describe land in the Kruger National Park (KNP) to serve as a basis for management planning and other ecological studies. To make the map and data suitable for these purposes, the KNP was subdivided into 56 land types on the basis of soil and vegetation patterns and landform characteristics. The land types were included into 11 land systems on the basis of geological, geomorphological and climatic characteristics. This land type map was used in my study to differentiate geological boundaries of the study herds.

- Gertenbach (1987) compiled a map of the KNP's landscapes providing a similar template to that of Venter (1990) for management planning and ecological studies. Subsequent analysis of the two studies by Solomon *et al*. (1999) showed a high degree of overlap in the two classification systems, whereby classified units share similar boundaries.

2.2 Materials and methods

2.2.1 Location of the feeding and control patch

We located buffalo herds fitted with VHF radio-collars using radio-telemetry equipment. We located the herds at least once a week, but often several times a week, as repeat sightings of the herd were often needed to locate feeding patches if the herds where busy with other behaviour e.g. walking, resting, drinking or low intensity feeding.

To minimise the impact on the herd's behaviour and movement, the sampling of the patches could not always be undertaken immediately after the herd had finished feeding, as they frequently chose to rest in close proximity to the patch. This often meant returning later in the day or, in the case of late afternoon observations, the next morning.

The patches were measured for two focal breeding herds, namely the Mavumbye herd (M), which occurred on the basalts, and the Timbavati herd (T), which occurred predominantly on the granites and gabbro intrusions. Both herds are named after the watercourses that dominate their home range. Patches were located every month, with an average of six patches sampled per month over the period of the study. Focal herds were identified by the presence of certain VHF radio collars whose home ranges encompassed the two dominant geological substrates. The Timbavati herd predominantly occurred on an underlying Granite basement complex; with Gabbro intrusions and the Mavumbye herd on a Basalt substrate.

The sampling was duplicated for a control site, neighbouring the selected feeding patch. The neighbouring control site was sampled at a distance of 100m perpendicular to the observed edge of the foraging path, alternating left and right of the patch for successive samples. A similar sampling strategy was employed by Stokke & du Toit (2000), where 50m was successfully used as the distance between control and experimental sites to determine elephant forage selection, and differentiate between bull and herd forage selection. The objective of the study was to determine what the patch selection criteria are for buffalo, when an array of habitat types are available to them within the landscape; and it was felt that this would be best achieved by using neighbouring sites. Buffalo herds in the central region vary in size from 300-1000 animals. Herds of this size often encompass a lateral area of a hundred metres or more, requiring the control patch to be located one hundred metres from the edge of the foraging path to avoid surveying the fringes of the foraging path.

The herd's activity was observed without the herd being aware of the observer's presence, to ensure no behavioural bias was introduced. A feeding patch was classified as any site where an "activity" scan, recorded in the form of an ethogram (i.e. recording a number of individuals exhibiting specific behaviour), of the herd shows a minimum of 75%-80% of the individuals to be feeding, or whose posture suggests such activity. Once these criteria were met and the herd had moved away, a vegetation survey was conducted in the centre of the foraging path, as noted by direct observation and spoor.

2.2.2 Technique used for vegetation sampling

The characteristics of the patch or stand were measured using a modified Braun Blanquet approach following Westfall *et al.* (1996) using scale-related area-based sampling, wherein plant species composition and growth form is recorded and cover determined using the Plant Number Scale (Westfall & Panagos, 1988). The method records every species and growth form (Westfall, 1992) within a 10mx20m quadrat. Quantifying the area of a patch is difficult and was not the objective of this study, but rather to sample the core area of the patch and determine its attributes. Casual observation revealed that the patches were often in the region of 20-50m wide and of a longer length. Hence, the sampling area of $200m^2$ was deemed adequate to be representative of the larger patch.

The Plant Number Scale (Westfall & Panagos, 1988; Westfall *et al*., 1996) method of determining plant canopy cover is a cover sampling method based on mean crown diameter and mean crown to crown spacing, derived from Edwards (1983) crown to gap ratios. The mean crown diameter determines cover-sampling transect length while the transect width is based on 4/5ths of the mean crown to crown gap. The number of individuals are counted within the transect and the percentage cover is read off a scale, according to the count. Thus, both plant spacing and crown size are taken into account in the cover sample. Scale increments are whole plants, resulting in a 33-class scale.

The advantages of the Plant Number Scale include increased precision compared with other visual class estimation techniques and skill development in visually estimating cover (Westfall, 1998).

The disadvantages include reduced precision in using crown diameter classes as opposed to precise crown measurements as well as insufficient variation being included within shorter transects (Westfall, 1998). A further disadvantage is the difficulty in determining mean crown to crown gap for plants with varied spacing. Spacing can vary considerably for plants with a given cover and density in terms of individuals per hectare (Westfall, 1998).

The Plant Number Scale has also been used successfully by Funston (1992) to determine habitat selection of buffalo in the Sabi-Sand Game Reserve.

As plant communities form a hierarchy, in which smaller plant communities can be included in larger plant communities, scale should be taken into account for the differentiation of plant communities; so that the floristic variation recorded is appropriate to the scale (Westfall *et al.*, 1996). Considering the size of the stand of vegetation (feeding patch) requiring characterisation, the scale of 1:12000 (Panagos, 1995) was chosen ensuring the appropriate measurement of floristic variation.

2.2.3 Methods used to analyse plant species data

Phytotab-PC version 1.01 (Westfall, 1997) software was used to analyse the data and determine plant units (phytosociological classification). The data were later reanalysed using an updated version of Phytotab-PC (Westfall *et al.*, 1997) for reasons outlined below.

Phytosociological classification is the orderly arrangement of relevés into plant communities, based on similarities in vegetation structure and floristic composition (Gabriel & Talbot, 1984). Alternately stated, a plant community is a group of plants, at a particular scale, sharing a common environment and distinguished by a particular floristic composition (Westfall *et al.*, 1996).

Phytotab-PC uses a two-way matrix to portray classified plant communities. Species are represented by rows and the relevés (patches) are arranged in columns. The value at the intercept of the column and row indicates species presence, while blank intercept values represent species absence. Each value quantifies the species in terms of cover or cover abundance (Westfall, 1992).

2.2.4 Relevé grouping

In order to investigate whether or not floristic differences existed between feeding and control sites, the total data set (both feeding and control sites combined) was analysed using Phytotab-PC. Should the floristics of the two treatments differ sufficiently; the resulting classification would result in feeding sites occurring in different communities to that of the control sites.

Based on the assumption that there is a compositional difference between feeding and control patches, one would expect 1) the feeding patch to always occur in another community type to it's control site and 2) the classification should never include feeding patches into a community type where control sites occur, i.e. Feeding and control sites would never occur in the same community type.

No manipulation (shifting) of community delimiters took place for this classification, to ensure an objective result.

The feeding sites and control sites were then classified individually (Appendix 12 and Appendix 13), in order to describe their floristic compositions, including diagnostic and key plant species. Derived data could also be obtained on quantifiable community variables, including grass phytomass, percentage canopy cover of dominant species and community structure (the percentage that each growth form represented in the community). Manual shifting of community delimiters had to take place to create tighter groups of species in this matrix. The ideal classification would be one where the groups of relevés form tight groups of species without gaps between the species occurrences, and with none of these species occurring outside of this grouping (Panagos, 1995). In practice however this seldom occurs, necessitating the need for manual manipulation of the community delimiters.

In order to describe the structural as well as floristic characteristics of buffalo habitats separate species numbers were assigned to the various growth forms (e.g. dwarf shrub, shrub or tree) of a specific species. This was done to overcome a shortcoming of Phytotab-PC, which does not allow duplicates of the same species within a given relevé to be computed. One would normally only retain one of the growth forms for a multiple species occurrence, and delete the others. The assigning of different species numbers to the individual growth forms of the same species, allowed the duplicates to be retained in the classification and provide a clearer description of the structural characteristics of the various communities.

2.2.5 Statistical analysis

2.2.5.1 Randomisation test

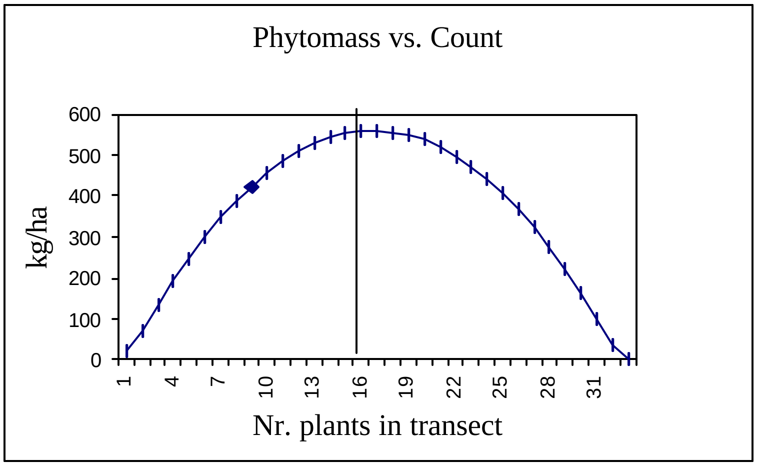
A randomisation test was used to evaluate whether the assignment of feeding patches and its paired control patch within each community type, approached a random assignment or not. To do this I ran 5000 simulations using code written in MATLAB 7.2. (Mathsoft ™).

The following algorithm was used:

1. Calculate the proportion of times the treatment and control sites are in the same community in the actual data.
2. Reshuffle the assignment of treatment and control randomly.
3. Calculate the proportion of times the treatment and control sites are in the same community in the randomised data from point number 2.
4. Repeat points 2 and 3, 5000 times.
5. Look at the number of simulations that produced more extreme values than that observed in point number 1 (i.e. the proportion of times the treatment and control sites are in the same community in the actual data).

2.2.6 Problems incurred with Phytotab-PC software

An intrinsic error in the phytomass calculation formula was discovered in Phytotab-PC ver. 1.01 (Figures 3 and 4). The formula is roughly based on the positive linear relationship between the number of plants counted in the belt transect, and that species' phytomass. This relationship held true only to a count of 16 plants, thereafter an inverse relationship was seen (Figure 3). Hence, the phytomass increased with increasing number of plants to a point of inflection, after which the phytomass decreased with increasing number of plants in the transect, until the phytomass was nil at a maximum count (32), which is equivalent to a canopy cover of 100%. This is not ecologically or mathematically plausible and was subsequently brought to the attention of the author and designer (Dr. R.H. Westfall) of the technique and software. Subsequent versions of the program have the corrected formula in place.



Figures 3: The relationship between phytomass and number of plants counted in the belt transect in the first (error in formula) version of Phytotab-PC (Westfall, 1988). Figure 3 highlights the error in the phytomass/count logarithm, whereby from a count of 16 plants in the variable length belt transect grass phytomass begins to decrease with an increasing number of plants counted.

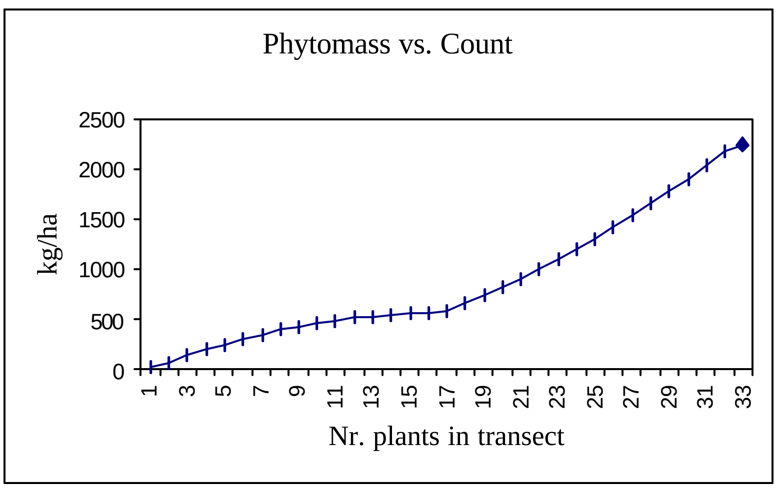


Figure 4: The relationship between phytomass and the number of plants counted in the belt transect, in the second version of Phytotab-PC, with the corrected algorithm. An ecologically plausible linear relationship is present.

The original error in this program does not pose a major problem when conducting a phytosociological classification, as a minimum number of four relevés, and often many more than that, are usually aggregated to form a vegetation community. This "smoothing effect" will be help buffer the effects of a high count for any given species, as the characteristics of that species will be averaged across all included relevés. As the inflection point occurs at a count of 16, it will be in only a very few instances where a count above this occurs.

In the context of this type of project it had the potential to influence the results, as one relevé (feeding patch) was being compared to another adjacent relevé (control patch) to investigate if any small-scale differences existed between the two. However, only 16 plants in 14 different relevés had a count of 16 of more; of the 2699 plant records and 172 relevés sampled, which equates to only 0.005% and 0.08% of records and relevés that may have been affected by this error, respectively. Nevertheless, the error was corrected and correct derivatives were generated for the high frequency plants in this study.

An additional error was discovered in the biomass algorithm. This occurs when Phytotab-PC generates grass phytomass values for each community, resulting in two phytomass values being generated for one of the species in the last community. This error has also subsequently been corrected in the program and hence in the biomass tables in this dissertation.

2.3 Results

2.3.1 Phytosociological classification

2.3.1.1 Classification combining Feeding and Control patches

Eighty-six feeding and eighty-six control patches were sampled over an 18-month period, 36 feeding and control patches were sampled for the Timbavati herd, 35 on Granite and one on basalt (the herd moved onto the basalts at the end of the dry season), and 52 feeding and control patches were sampled for the Mavumbye herd, all on Basalt substrates.

The phytosociological delineation of the Feeding and Control relevés (sampling units or quadrats) yielded 28 plant communities (Appendix 11).

All feeding sites and control sites were not separated into different plant communities after community delineation, meaning that there was some overlap in species composition between feeding patches and control sites over the duration of the study (see Appendix 11).

Twenty-three (26.75%) of the eighty-six feeding patches sampled occurred within the same community type as its control site. Conversely, 73.25% of the feeding patches occurred in different community types to their control sites; showing that a difference in species composition or structure existed between a large majority of the feeding and control patches, when considered as a paired sample e.g. relevé 1A (control) and relevé 1 (feeding) occurred in different communities. This in itself is note worthy for a claimed bulk-feeder considering the relatively fine sampling scale.

Feeding and control patches occurred together in each of the twenty-eight communities (though not necessarily the experimental and its control counterpart). This means that when feeding and control treatments are considered on a non-pair-wise basis, but rather as two groups, they share similar floristics.

While a degree of overlap exists in the floristics of feeding and control patches, phytosociological classifications only take cognisance of the presence or absence of a given species when classifying communities, and not their relative or absolute abundances. Thus a perennial grass or woody plant occurring in a number of sites with a high cover/abundance has the same influence on a classification as an annual grass or ephemeral forb with a low cover/abundance, also occurring in a number of sites. This was observed in this classification in certain communities whereby a species that was diagnostic according to the classification due to its occurrence in a number of relevés for a given community, occurred at a very low abundance in each relevé. One example would be the occurrence of *Ormocarpum trichocarpum* at lowest recordable abundance in community 15, yet it emerges as one of the diagnostic species for that community.

2.3.1.1.1 Results of randomisation test

In the actual data 27% of the time the control and treatment sites are in the same community (or 73% of the time they are in different communities). If you randomly assign feeding and control sites to the different communities, on average they would be in the same community 12% of the time. Thus, in the observed data treatment and control sites are more often seen in the same community than you might expect.

2.3.1.2 Classification of feeding patches

Phytosociological delineation of only the feeding patches was done to describe buffalo habitat characteristics, yielding 5 communities. Some of the statistics pertaining to the classification are as follows:

Total relevés: 86	Total communities: 5
Total species: 200	Total species groups: 13
Total diagnostic species: 104	Total non-diagnostic species: 96
Diagnostic proportion: 52%	

Community types

The following communities have been named according to the following guidelines:

i) The diagnostic graminoid and woody plant for each community.

ii) The vegetation structure classified according to the criteria set out by Edwards (1983).

iii) The dominant underlying substrate for each community, determined using Arcview©3.2a to superimpose sampling points onto the underlying Land Types (Venter, 1990) data layer.

2.3.1.2.1 Community types on Basalt underlying geology – Mavumbye herd

A. Community 1

Shrub *Combretum mossambicense/Aristida adscensionis* Tall Sparse Shrubland community on Basalt substrate.

This was the largest community, consisting of the greatest number of relevés (32). The community included almost exclusively, patches that occurred on Basalt derived soils, utilised by the Mavumbye herd. Two of the Timbavati herd's patches also fall into this community; one on a Gabbro derived soil, also high in clay content and thus exhibited similar vegetative characteristics, and the other on Basalt. The Basalt patch used by Timabavati occurred during the dry season of 2002, when the herd moved significant distances in order to find suitable forage. This community predominantly characterised the vegetation characteristics of the Midslope and Footslope feeding patches. A summary of the relevés constituting this community are listed in Table 2.

Community statistics

Total relevés in community: 32

Total species in community: 85

Total diagnostic species in community: 55

Diagnostic proportion: 64.71%

Species richness in terms of mean species per relevé: 14

Table 2: List of relevés that constitute this community and their respective catena positions, Land Type classification (Venter, 1990), season sampled, herd affiliation and aspect.

Relevé	Catena	Land Type	Herd	Aspect	Geology	Season
2	Footslope	Satara	M	East	Basalt	Late wet
4	Midslope	Satara	M	South-East	Basalt	Late wet
17	Midslope	Satara	M	North-West	Basalt	Early dry
61	Footslope	Mavumbye	M	East	Basalt	Late wet
18	Midslope	Mavumbye	M	South-West	Basalt	Early dry
5	Footslope	Satara	M	South-East	Basalt	Early dry

13	Crest	Satara	M	North-West	Basalt	Early dry
24	Midslope	Mavumbye	M	South-East	Basalt	Late dry
32	Midslope	Mavumbye	M	East	Basalt	Late dry
19	Midslope	Satara	M	West	Basalt	Early dry
20	Midslope	Satara	M	West	Basalt	Early dry
85	Valley bottom	Mavumbye	M	South	Basalt	Late dry
58	Footslope	Satara	M	East	Basalt	Late wet
49	Midslope	Satara	M	South-West	Basalt	Early wet
84	Footslope	Satara	M	East	Basalt	Late dry
83	Midslope	Satara	M	West	Basalt	Late dry
59	Crest	Satara	M	North-West	Basalt	Late wet
51	Midslope	Satara	M	East	Basalt	Early wet
80	Midslope	Satara	M	West	Basalt	Early dry
47	Crest	Mavumbye	M	North	Basalt	Early wet
46	Midslope	Mavumbye	M	East	Basalt	Early wet
29	Midslope	Satara	M	East	Basalt	Late dry
77	Footslope	Mavumbye	M	North	Basalt	Early dry
79	Crest	Orpen	T	North	Gabbro	Early dry
73	Midslope	Mavumbye	M	South-East	Basalt	Late wet
78	Crest	Satara	M	South-East	Basalt	Early dry
70	Midslope	Satara	M	South-East	Basalt	Late wet
74	Crest	Mavumbye	M	East	Basalt	Late wet
71	Midslope	Mavumbye	M	East	Basalt	Late wet
50	Midslope	Satara	M	South	Basalt	Early wet
68	Footslope	Satara	M	South	Basalt	Late wet
42	Footslope	Satara	T	North-East	Basalt	Late dry

Key species of community

The “Key species” file is extracted from the “Community Composition Analysis” output file of Phytotab-PC. Key species are those classified as strong and weak competitors, which are those species that lie outside, above (strong) and below (weak), the standard errors of the means for the regressions of cover to frequency ratios for the species of each growth form class within each community.

Only the strong competitors are reflected in Table 3.

The key species for this community are those relatively diagnostic for the substrates they occurred on. Due to the clay properties of the soil very few large trees are found in this community, but rather their stunted forms e.g. *A. nigrescens.* The most widespread grass across the catenal sequence was *Setaria incrassata* that can be found commonly from the valley bottoms through to the crests. It is often associated with areas of temporary or seasonal water inundation (van Oudtshoorn, 1999). The footslopes were prolific with *Sporobolus ioclados,* while in the slightly more degraded and well-utilised patches *Urochloa mosambicensis* was dominant.

Table 3: Key species/Strong competitors for each growth form class:

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
	Dichrostachys cinerea	*Acacia nigrescens*	*Setaria incrassata*	*Hemizygia petrensis*
	Combretum mossambicense		*Urochloa mosambicensis*	*Heliotropicum steudneri*
			Sporobolus cunsimilis	
			Sporobolus ioclados	

Dominant species of community

This application in the Phytotab-PC program requires a percentage canopy cover value be entered as a "cut-off", below which species are excluded from the "Dominant" class. I subjectively chose 0.1% as the cut-off, which then only included a few species that I felt would truly reflect the dominant species for that community type; namely those with above average canopy covers. *Urochloa mosambicensis* was the most dominant grass species of this community. A list of the dominant species for this community appears in Table 4.

Table 4: Dominant species in community with respect to percentage canopy cover (only top three listed)

Species	% Canopy cover
Urochloa mosambicensis	5.46
Panicum maximum	2.65
Setaria incrassata	2.55

Grass biomass

Mean grass phytomass estimates, illustrates the abundance of species in this community (Table 5). The grass species listed as dominant species for this community also compute the highest biomass figures.

Table 5: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Eragrostis rigidior	0.00	0.64
Aristida congesta subsp. *barbicollis*	0.00	0.64
Sorghum versicolor	0.00	0.64
Urochloa panicoides	0.00	2.14
Enneapogon scoparius	0.00	2.84
Fingerhuthia africana	0.01	4.29
Eragrostis superba	0.00	4.92
Brachiaria eruciformis	0.03	6.04
Brachiaria deflexa	0.02	7.68
Chloris virgata	0.05	9.90
Enneapogon cenchroides	0.06	12.05
Bothriochloa insculpta	0.07	15.44
Aristida adscensionis	0.08	16.57
Heteropogon contortus	0.17	17.64
Ischaemum afrum	0.21	22.01

Schmidtia pappophoroides	0.28	25.51
Sporobolus ioclados	1.26	28.23
Bothriochloa radicans	0.29	41.61
Digitaria eriantha	0.29	43.00
Cenchrus ciliaris	0.8	62.55
Themeda triandra	0.81	77.92
Panicum coloratum	0.59	104.42
Setaria incrassata	2.55	133.09
Panicum maximum	2.65	178.10
Urochloa mosambicensis	5.46	215.04
Totals:	15.67	1033.07

Community structure

The woody layer was composed of very few trees with sparse shrubs and dwarf shrubs and a moderate under storey of grass. A quantitative and graphical breakdown of the community structure is provided in Table 6 and Figure 5 respectively.

Table 6: Community structure arranged by growth form. Cover values represent projected crown cover:

Growth form	Cover	Proportion
Tree	0.00%	0.01%
Shrub	0.16%	0.92%
Dwarf shrub	0.36%	2.02%
Grass	15.67%	89.32%
Forb	1.36%	7.73%
Total class cover	17.54%	

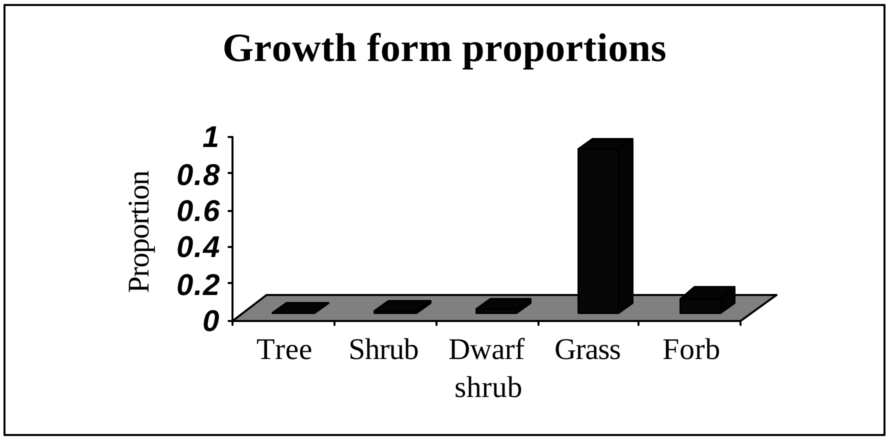


Figure 5: Histogram showing the proportional cover of each growth form in community.

B. Community 2

Shrub *Gymnosporia buxifolia/Enneapogon scoparius* Tall Sparse Shrubland on Basalt.

This community consists of 15 relevés, 14 situated on Basalt derived soils, and one on gabbro substrate; this being the only relevé utilised by the Timbavati herd in this community. The herbaceous layer has a moderate canopy cover with four of the top five preferred species occurring at the highest biomass. This community is comprised of predominantly footslope and valley bottom reaches. A full list of the relevés constituting this community appears in Table 7.

<u>Community statistics</u>

Total relevés in community: 15

Total species in community: 82

Total diagnostic species in community: 53

Diagnostic proportion: 64.63%

Species richness in terms of mean species per relevé: 14

Table 7: List of relevés that constitute this community and their respective catena position, Land Type classification (Venter, 1990), season sampled and aspect.

Relevé	Catena	Land Type	Herd	Aspect	Geology	Season
30	Footslope	Mavumbye	M	North	Basalt	Late dry
36	Footslope	Mavumbye	M	West	Basalt	Late dry
27	Valley bottom	Mavumbye	M	East	Basalt	Early dry
35	Footslope	Mavumbye	M	No data	Basalt	Late dry
1	Midslope	Mavumbye	M	South-East	Basalt	Late wet
39	Crest	Satara	M	South-West	Basalt	Late dry
7	Midslope	Mavumbye	M	East	Basalt	Late wet
65	Valley bottom	Mavumbye	M	South	Basalt	Late wet
41	Midslope	Satara	M	West	Basalt	Late dry
60	Footslope	Satara	M	South-West	Basalt	Late wet
8	Midslope	Mavumbye	M	East	Basalt	Late wet
57	Valley bottom	Satara	M	South	Basalt	Early wet
22	Valley bottom	Orpen	T	North	Gabbro	Early dry
86	Valley bottom	Mavumbye	M	East	Basalt	Early dry
44	Footslope	Satara	M	North	Basalt	Late dry

Key species

The key species for this community (Table 8.) are all diagnostic for the lower reach catenal positions. Larger trees are a feature of this community along the valley bottom. The two *Sporobolus* species were widespread along the lower reaches. *Urochloa mosambicensis* again emerges as a key species for this community.

Table 8: Key Species/Strong Competitors for each growth form class:

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
Lonchocarpus capassa	*Acacia tortillis*	*Acacia nigrescens*	*Sporobolus ioclados*	*Vernonia* sp.
		Flueggea virosa	*Urochloa mosambicensis*	
			Cenchrus ciliaris	
			Sporobolus cunsimilis	

<u>Dominant species</u>

Of the three species listed in Table 9. *Sporobolus cunsimilis* did not occur in many feeding patches. Due to most of the patches in this community occurring in the lower catenal reaches, both *Sporobolus* sp. feature strongly along with *Cenchrus ciliaris.*

Table 9: Dominant species in community with respect to percentage canopy cover

Species	% Canopy Cover
Cenchrus ciliaris	2.37
Urochloa mosambicensis	2.31
Sporobolus cunsimilis	1.94

<u>Grass biomass</u>

Urochloa mosambicensis and *Cenchrus ciliaris* had the highest phytomass in this community. The complete species list of grass biomass estimates appears in Table 10.

Table 10: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Aristida adscensionis	0	1.48
Aristida congesta subsp. *congesta*	0	1.48
Dactyloctenium aegyptium	0	1.48
Eragrostis cilianensis	0	1.48
Bothriochloa insculpta	0	4.44
Cyperus sp.	0.03	8.85
Aristida congesta subsp. *barbicollis*	0.03	16.38
Ischaemum afrum	0.17	19.95
Bothriochloa radicans	0.11	22.61
Setaria incrassata	0.06	23.76
Enneapogon cenchroides	0.24	24.52
Heteropogon contortus	0.24	27.48
Sporobolus cunsimilis	1.94	43.50
Eragrostis superba	0.23	45.29
Schmidtia pappophoroides	0.42	47.57
Digitaria eriantha	0.78	53.36
Panicum coloratum	0.3	57.62
Enneapogon scoparius	1.06	58.47
Sporobolus ioclados	1.3	68.59
Themeda triandra	0.42	77.49
Panicum maximum	0.61	114.05
Cenchrus ciliaris	2.37	152.28
Urochloa mosambicensis	2.31	182.13
Totals:	12.63	1054.24

Community structure

Trees form an integral structural component of this community with shrubs and dwarf shrubs largely absent in the understorey (Table 11). The absence of smaller woody growth forms reduces the overall woody density. This community has a relatively high grass biomass (Figure 6).

Table 11: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.04%	0.34%
Shrub	0.11%	0.86%
Dwarf shrub	0.11%	0.82%
Grass	12.63%	96.15%
Forb	0.24%	1.83%
Total class cover	13.13%	

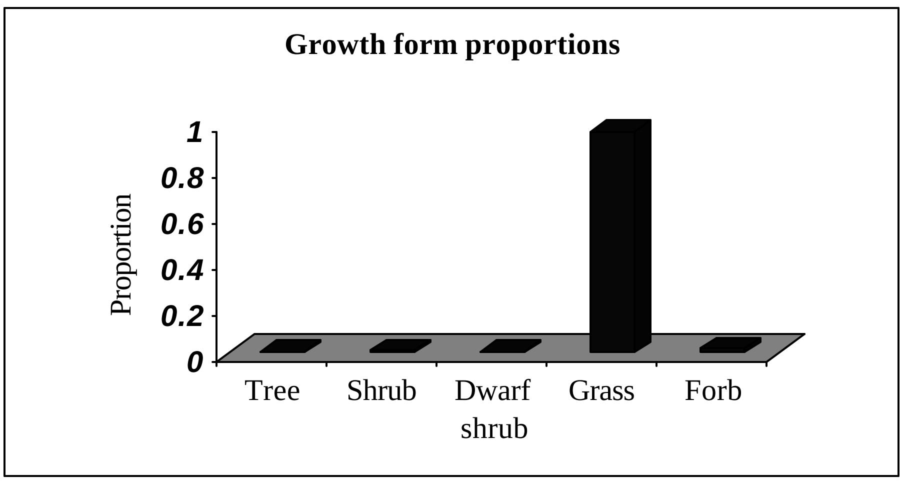


Figure 6: Histogram showing the proportion each growth form contributes to the community.

C. Community 3

Dwarf shrub *Acacia xanthophloea/Sporobolus cunsimilis* Tall Sparse Shrubland community on Basalt.

This predominantly wet season community was composed of patches of the lower reaches of the hillslope sequence. The community is floristically fairly distinct from the other two communities of the Mavumbye herd, due to the dominance of riverine species, especially those found in the river channel. Structurally woody plants are largely absent from the community with a very high herbaceous content. A full list of the relevés for this community appears in Table 12.

<u>Community statistics</u>

Total relevés in community: 6

Total species in community: 21

Total diagnostic species in community: 8

Diagnostic proportion: 38.10%

Species richness in terms of mean species per relevé: 5

Table 12: List of relevés that constitute this community and their respective catena positions and Land Type classification (Venter, 1990).

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
3	Footslope	Satara	Wet	M	East	Basalt
6	Footslope	Mavumbye	Wet	M	South	Basalt
12	Footslope	Mavumbye	Dry	M	South-West	Basalt
62	Footslope	Mavumbye	Wet	M	South	Basalt
54	Valley bottom	Satara	Wet	M	South-West	Basalt
23	Valley bottom	Mavumbye	Dry	M	North-East	Basalt

<u>Key species</u>

The only two key species were *Sporobolus ioclados* and *Cenchrus ciliaris*, both of which are prolific on these substrates. No other growth form featured as a key species for Community 2 (Table 13).

Table 13: Key Species/Strong Competitors for each growth form class:

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
			Sporobolus ioclados	
			Cenchrus ciliaris	

Dominant species

Sporobolus cunsimilis and *Sporobolus ioclados* both exhibit very high canopy covers in this community, resulting largely in their aerial dominance of the herbaceous layer. *S. cunsimilis* is an abundant grass in the perennial drainage systems of the area, and its overwhelming presence in feeding patches is a result of its proximity to drinking water. The dominant grass species for this community are listed in Table 14.

Table 14: Dominant species in community with respect to percentage canopy cover

Species	% Canopy Cover
Sporobolus cunsimilis	9.26
Sporobolus ioclados	8.23
Cenchrus ciliaris	3.78

Grass biomass

Sporobolus ioclados and *Sporobolus cunsimilis* comprise 56 percent of the total community grass biomass. *Panicum coloratum* and *Urochloa mosambicensis* also have relatively high biomass estimates in comparison to the balance of the grasses in the community (Table 15).

Table 15: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Ischaemum afrum	0	3.70
Heteropogon contortus	0	3.70
Chloris gayana	0	3.70
Unknown sp.	0	3.70
Brachiaria nigropedata	0.02	11.44
Chloris pycnothrix	0.07	22.13
Panicum maximum	0.07	25.83
Setaria incrassata	1.08	74.46
Cenchrus ciliaris	3.78	93.16
Urochloa mosambicensis	1.09	105.94
Panicum coloratum	1.09	109.64
Sporobolus ioclados	8.23	266.12
Sporobolus cunsimilis	9.26	325.30
Totals:	24.69	1048.80

Community structure

The community structure is composed almost exclusively of grass, with a minor contribution of shrubs. Table 16 and Figure 7 provide quantitative and graphical data on community structure.

Table 16: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.00%	0.01%
Shrub	0.42%	1.68%
Dwarf shrub	0.00%	0.02%
Grass	24.69%	98.22%
Forb	0.02%	0.07%
Total class cover	25.14%	

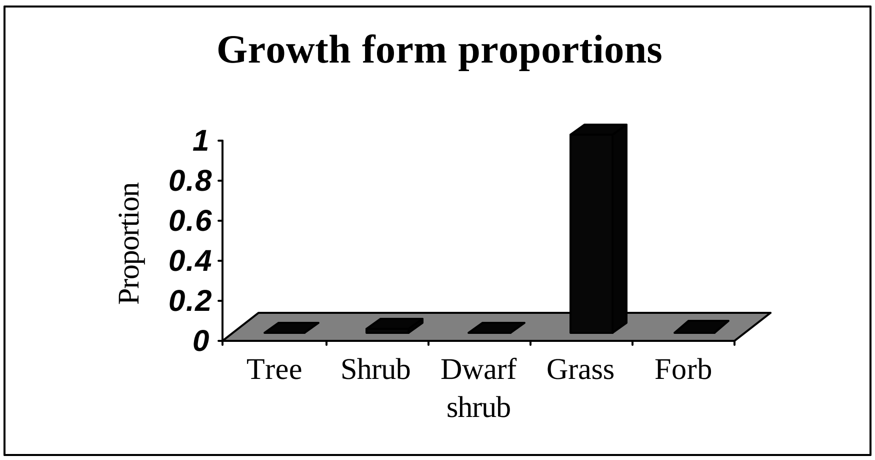


Figure 7: Histogram showing the proportion each growth form contributes to the community.

2.3.1.2.2 Community types on Granite underlying substrate – Timbavati herd

D. Community 4

Tree *Acacia gerrardii/Eragrostis trichophora* Low sparse woodland community on Gabbro and Gneiss.

This community is predominantly on the Gabbro Landtype, with one patch occurring on the Ecca Shale sedimentary soils. During the extreme dry conditions of 2002, the Timbavati herd moved into the neighbouring Manyeleti provincial game reserve, located on the western boundary of the study area. No fences restrict game movement between the two reserves and as such two of the feeding patches occurred in the Manyeleti. Venter

(1990) did not classify the neighbouring private and provincial reserves, comprising the Greater Kruger National Park, and as such a Land Type classification for them does not exist. Hence, the geological affiliation for these two feeding patches was inferred from the neighbouring Land Type within the KNP. The majority of the patches occurred on midslopes over the wet season, when water availability was not a limiting factor and herds could source patches further away from perennial water sources. The subsequent species assemblages thus represent patches on the arid end of a continuum. Despite the different underlying geology, the presence of the same dominant species found in patches on basalts, can be seen on the granitic soils too. The full list of relevés in this community appears in Table 17.

<u>Community statistics</u>

Total relevés in community: 10

Total species in community: 80

Total diagnostic species in community: 60

Diagnostic proportion: 75%

Species richness in terms of mean species per relevé: 23

Table 17: List of relevés that constitute this community and their respective catena positions, Land Type classification (Venter, 1990), season sampled and aspect.

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
53	Midslope	Orpen	Wet	T	East	Gabbro
67	Midslope	Muzandzeni	Wet	T	East	Gneiss
63	Midslope	Manyeleti*	Wet	T	West	Gneiss
75	Footslope	Orpen	Wet	T	North	Gabbro
76	Midslope	Orpen	Wet	T	South	Gabbro
48	Midslope	Vutome	Wet	T	North-West	Ecca-shale
11	Footslope	Orpen	Wet	T	South	Gabbro
66	Valley bottom	Muzandzeni	Wet	T	East	Gneiss
64	Footslope	Manyeleti*	Wet	T	North-East	Gneiss
81	Midslope	Orpen	Dry	T	East	Gabbro

Key species

Acacia gerrardii is a key component of this community, especially common on the gneiss-derived soils. A mixture of fine-leaved (*Acacia* sp. and *Dichrostachys cinerea*) and broad-leaved (*Combretum apiculatum* and *Bolusanthus speciosus*) plants characterise the woody component of this community. *Digitaria eriantha*, with its high leaf proportion, is the only key grass species. *Digitaria eriantha* commonly occurs on these Land Types where rocky areas abound, made possible due to its stoloniferous root system (where other grasses have difficulty establishing themselves) as well as sandy and gravelly soils (van Oudtshoorn, 1999); conditions that are common in granitic areas. Table 18 lists all the key species for this community.

Table 18: Key Species/Strong Competitors for each growth form class.

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
Acacia gerraddii	*Dichrostachys cinerea*	*Acacia nigrescens*	*Digitaria eriantha*	*Indigofera sp.*
	Combretum apiculatum	*Acacia karroo*		
		Bolusanthus speciosus		

Dominant species

Digitaria eriantha was the most dominant species (Table 19). Forbs are common on the sandy soils with species of the *Indigofera* genus especially prolific in the wet months. *Themeda triandra* was often present in feeding patch communities, even though buffalo only feed moderately on it (Macandza *et al.*, 2004).

Table 19: Dominant species in community with respect to percentage canopy cover.

Species	% Canopy Cover
Digitaria eriantha	2.65
Indigofera sp.	2.59
Themeda triandra	1.19

Grass biomass

As the classification of this community implies - low open grassland - the standing crop of grass was relatively low despite the literal absence of competing woody plants. This can be ascribed in part to the dominant species of the community *Urochloa mosambicensis*, having a low sprawling growth form that is not conducive to the build-up of biomass. *Digitaria eriantha* was the grass species with the highest biomass in this community (Table 20).

Table 20: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Aristida congesta subsp. *barbicollis*	0	2.22
Panicum deustum	0	2.22
Enneapogon scoparius	0.01	9.08
Eragrostis trichophora	0.01	9.08
Brachiaria deflexa	0.01	9.08
Sporobolus ioclados	0.01	9.08
Eragrostis rigidior	0.04	17.71
Cenchrus ciliaris	0.09	19.34
Schmidtia pappophoroides	0.1	28.42
Brachiaria nigropedata	0.08	28.77
Heteropogon contortus	0.08	35.43
Bothriochloa radicans	0.08	40.73
Eragrostis superba	0.28	68.98
Urochloa mosambicensis	0.43	80.29
Panicum maximum	1	119.43
Panicum coloratum	0.82	135.45
Cymbopogon plurinodis	0.81	140.61
Themeda triandra	1.19	174.6
Digitaria eriantha	2.65	232.21
Totals:	7.69	1162.73

Community structure

Woody plants contribute strongly to the community structure. The grass proportion was relatively low with a high proportion of forbs present in the substratum. Table 21 and Figure 8 provide quantitative and graphical representation of the community structure respectively.

Table 21: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.88%	6.81%
Shrub	0.40%	3.13%
Dwarf shrub	0.87%	6.78%
Grass	7.69%	59.84%
Forb	3.01%	23.44%
Total class cover	12.86%	

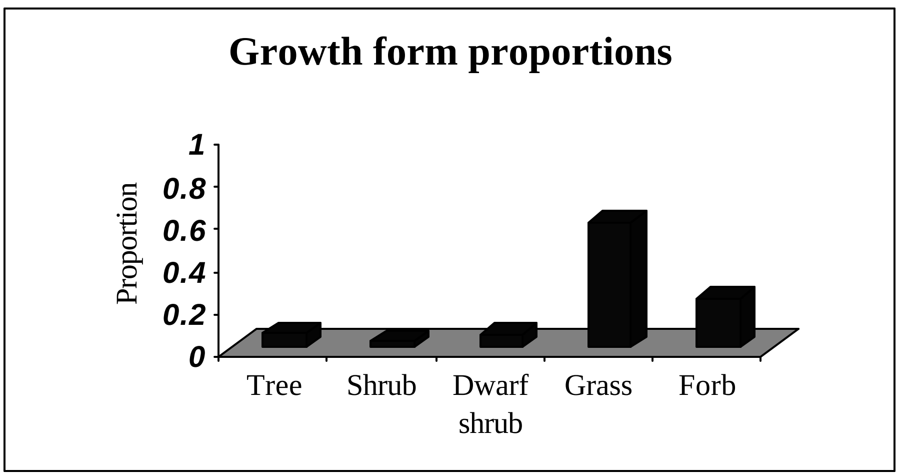


Figure 8: Histogram showing the proportion each growth form contributes to the community.

E. Community 5

Dwarf shrub *Gymnosporia buxifolia/Urochloa oligotricha* Low Sparse Woodland community on Gabbro and Gneiss.

Six of the twenty-three relevés occurred on Gneiss, and one on Ecca Shale, with the majority of patches occurring on Gabbro substrate. The geomorphological units are spread across all positions, but the majority are made up of midslopes. Community four represented the wet season selection of patches on the granitic soils, while this community largely represents the dry season feeding patch community. Table 22 lists all the relevés, as well as several of their attributes, of the community.

Community statistics

Total relevés in community: 23

Total species in community: 113

Total diagnostic species in community: 67

Diagnostic proportion: 59.29%

Species richness in terms of mean species per relevé: 18

Table 22: List of relevés that constitute this community and their respective catena positions, Land Type classification (Venter, 1990), season sampled and aspect.

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
55	Valley bottom	Muzandzeni	Wet	T	North	Gneiss
69	Crest	Muzandzeni	Wet	T	South	Gneiss
82	Footslope	Orpen	Dry	T	South	Gabbro
45	Crest	Vutome	Dry	T	East	Ecca-shale
21	Valley bottom	Orpen	Dry	T	North	Gabbro
37	Valley bottom	Muzandzeni	Dry	T	East	Gneiss
72	Midslope	Orpen	Wet	T	East	Gabbro
33	Midslope	Muzandzeni	Dry	T	South-East	Gneiss
43	Footslope	Muzandzeni	Dry	T	North	Gneiss
26	Midslope (lower)	Orpen	Dry	T	North	Gabbro
25	Midslope	Muzandzeni	Dry	T	North	Gneiss
28	Midslope	Muzandzeni	Dry	T	East	Gneiss
31	Midslope	Orpen	Dry	T	North-West	Gabbro
56	Midslope	Muzandzeni	Wet	T	East	Gneiss
16	Crest	Orpen	Dry	T	West	Gabbro

38	Crest	Muzandzeni	Dry	T	South-East	Gneiss
40	Midslope	Orpen	Dry	T	North	Gabbro
52	Crest	Orpen	Wet	T	North	Gabbro
15	Footslope	Orpen	Dry	T	North-West	Gabbro
34	Midslope	Orpen	Dry	T	North	Gabbro
10	Footslope	Orpen	Wet	T	North-West	Gabbro
9	Midslope	Orpen	Wet	T	South-East	Gabbro
14	Footslope	Orpen	Dry	T	North	Gabbro

Key species

Due to the majority of the patches occurring in the upper reaches of the hillslope, broad-leaved plants are strongly represented in this community. The selection of the herds for patches in sandy soils over the dry season may relate to the soil's lower CEC (cation exchange capacity) making more soil moisture available to rooted plants that may in turn result in greener plants. Woody plants dominate the key species for this community due to their relative abundance. The grass *Digitaria eriantha* again features as an integral component of feeding patches on sandier soils. Forb ratios are also high. The full list of Key Species appears in Table 23.

Table 23: Key Species/Strong Competitors for each growth form class.

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
Combretum apiculatum	*Combretum hereroense*	*Acacia exuvialis*	*Sporobolus ioclados*	*Indigofera* sp.
	Dalbergia melanoxylon	*Ximenia americana*	*Digitaria eriantha*	Yellow cluster look-alike
	Euclea divinorum			*Abutilon* sp.

Dominant species

In spite of the strong presence of woody plants in this community, grasses contributed the most to the overall percentage canopy cover. *Digitaria eriantha* was once again the most dominant species in patches utilised by the Timbavati herd. The two grass species that computed dominant for this community are listed in Table 24.

Table 24: Dominant species in community with respect to percentage canopy cover.

Species	% Canopy Cover
Digitaria eriantha	4.99
Themeda triandra	1.94
Urochloa mosambicensis	1.35

Grass biomass

This community had the highest mean grass biomass of any of the communities, which consisted predominantly of preferred species (Macandza *et al*., 2004). The other species occurring in the patch were of a very low biomass (Table 25).

Table 25: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Enneapogon scoparius	0	0.97
Eragrostis look-alike	0	0.97
Chloris gayana	0	0.97
Eragrostis trichophora	0	0.97
Brachiaria nigropedata	0	0.97
Cymbopogon excavatus	0	1.93
Perotis patens	0	2.98
Chloris mossambicensis	0	2.98
Unidentifiable	0	2.98
Aristida congesta subsp. *congesta*	0	3.95
Eragrostis cilianensis	0	3.95
Pogonarthria squarrosa	0.01	5.88
Melinis repens	0.04	8.41
Bothriochloa insculpta	0.02	8.76
Melinis repens	0.04	9.37
Ischaemum afrum	0.04	11.39
Aristida congesta subsp. *barbicollis*	0.06	17.07
Eragrostis rigidior	0.03	19.55

Sporobolus ioclados	1.12	25.14
Schmidtia pappophoroides	0.14	25.54
Urochloa oligotricha	0.26	30.16
Setaria incrassata	0.26	39.29
Bothriochloa radicans	0.4	43.54
Heteropogon contortus	0.26	57.60
Eragrostis superba	0.3	68.36
Cymbopogon plurinodis	0.43	76.60
Panicum coloratum	0.66	79.66
Panicum maximum	0.72	96.92
Urochloa mosambicensis	1.35	161.09
Themeda triandra	1.94	164.63
Digitaria eriantha	4.99	276.49
Totals:	13.1	1249.03

<u>Community structure</u>

The plant structure of this community largely typifies the overriding feeding patch structural characteristics by there being a dominant herbaceous layer interwoven with dwarf shrubs, shrubs and the intermittent tree.

The overall structure of this community concurs with previous South African studies whereby open grasslands and bushveld habitats are those generally preferred by buffalo. (Ryan, Knechtel & Getz, 2006; Funston *et al.*, 1994). The proportion each growth contributed to the overall community structure are presented in Table 26 and Figure 9.

Table 26: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.89%	5.20%
Shrub	1.62%	9.46%
Dwarf shrub	0.94%	5.48%
Grass	13.06%	76.18%
Forb	0.63%	3.68%
Total class cover	17.15%	

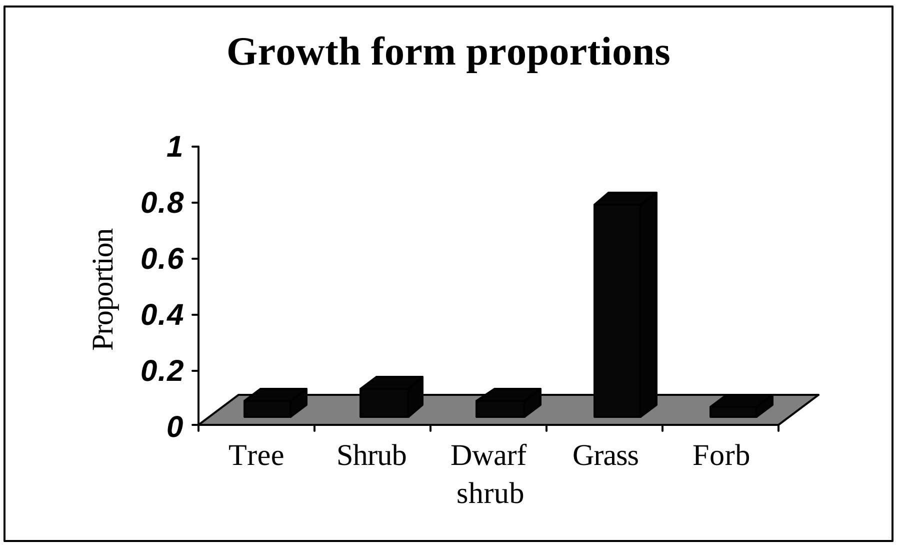


Figure 9: Histogram showing the proportion each growth form contributes to the community.

2.3.1.3 Classification of control patches

2.3.1.3.1 Community types on Granite substrate

F. Community 1

Dwarf shrub *Combretum apiculatum*/*Urochloa oligotricha* Low Open Woodland community on predominantly Gabbro and Gneiss.

This community is composed of upper slope patches. As a majority of feeding patches occurred on the lower reaches of the hillslope sequence, the neighbouring control patches often fell on higher reaches. Six of the patches are affiliated to the Mavumbye herd occurring on the basalt plains, however the majority of the patches were measured on the granite soils. Two avoided grass species (Macandza *et al*., 2004) occur as dominant species in this community namely, *Bothriochloa radicans* and *Eragrostis rigidior.* While a large overlap in the presence and absence of species occurs between feeding patches and their controls, normally avoided species feature dominantly in control patches. This alludes to the fact that one of the dominant selection criteria for buffalo may be a critical mass of preferred species in relation to avoided ones. This is supported by the high species diversity seen in this community across all growth forms. Woody structure is dominant with high projected canopy covers for both trees and dwarf shrubs. Table 27 provides a list of all the relevés constituting this community.

Community statistics

Total relevés in community: 33

Total species in community: 127

Total diagnostic species in community: 51

Diagnostic proportion: 40.16%

Species richness in terms of mean species per relevé: 19

Table 27: List of relevés that constitute this community and their respective catena positions and Land Type classification (Venter, 1990).

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
1	Midslope (upper)	Mavumbye	Wet	M	South	Basalt
34	Midslope	Orpen	Dry	T	North-West	Gabbro
22	Midslope	Orpen	Dry	T	North	Gabbro
41	Midslope	Satara	Dry	M	West	Basalt
21	Footslope	Orpen	Dry	T	North-West	Gabbro
59	Crest	Satara	Wet	Ma17	West	Basalt
78	Crest	Satara	Dry	M	South-East	Basalt
40	Crest (lower)	Orpen	Dry	T	North	Gabbro
10	Crest	Orpen	Wet	T	North	Gabbro
9	Crest	Orpen	Wet	T	South-East	Gabbro
49	Crest	Satara	Wet	M	South	Basalt
43	Midslope	Muzandzeni	Dry	T	South	Gneiss

37	Midslope	Muzandzeni	Dry	T	North	Gneiss
55	Crest	Muzandzeni	Wet	Td1	North-East	Gneiss
58	Midslope	Satara	Wet	M	East	Basalt
52	Crest	Orpen	Wet	T	North-East	Gabbro
16	Midslope	Orpen	Dry	T	West	Gabbro
28	Crest	Muzandzeni	Dry	T	North-East	Gneiss
11	Crest	Orpen	Wet	T	East	Gabbro
64	Seepline	Manyeleti*	Wet	S	East	Gneiss
63	Midslope (lower)	Manyeleti*	Wet	S	West	Gneiss
15	Footslope	Orpen	Dry	T	South-East	Gabbro
29	Footslope	Satara	Dry	M	South-West	Basalt
56	Crest	Muzandzeni	Wet	Td1	South	Gneiss
31	Midslope	Orpen	Dry	T	West	Gabbro
33	Footslope (on midslope)	Muzandzeni	Dry	T	West	Gneiss
81	Midslope (lower)	Orpen	Dry	Sa38	West	Gabbro
72	Crest	Orpen	Wet	S	North	Gabbro
69	Midslope	Muzandzeni	Wet	S	South-East	Gneiss
66	Midslope	Muzandzeni	Wet	S	North	Gneiss
25	Midslope	Orpen	Dry	Tb3	South-East	Gabbro
82	Midslope	Orpen	Dry	Sa38	North	Gabbro
75	Midslope (upper)	Orpen	Wet	S	East	Gabbro

Key species

Digitaria eriantha occurred in both feeding patch communities on granite substrate, and also dominates in this control community. *Bothriochloa radicans* and *Eragrostis rigidior* occur as key species in this community. A number of woody plants also hold key positions in the community, due to the high projected canopy covers of these growth forms. The full list of Key Species for the community appears in Table 28.

Table 28: Key Species/Strong Competitors for each growth form class.

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
Acacia nigrescens	*Combretum apiculatum*	*Peltophorum africanum*	*Digitaria eriantha*	*Heliotropicum steudneri*
	Acacia exuvialis	*Acacia nigrescens*	*Bothriochloa radicans*	
			Eragrostis rigidior	

Dominant species

Digitaria eriantha was the most dominant grass in this community. *Bothriochloa radicans* was the second most dominant plant in the patch, marginally more so than *Themeda triandra* (see Table 29).

Table 29: Dominant species in community with respect to percentage canopy cover.

Species	% Canopy Cover
Digitaria eriantha	2.71
Bothriochloa radicans	1.58
Themeda triandra	1.41

Grass biomass

Digitaria eriantha accounted for the highest grass biomass in this community. This community had high grass species diversity (see Table 30), particularly with a high number of unpalatable species (van Oudtshoorn, 1999).

Table 30: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Fingerhuthia africana	0	0.67
Chloris gayana	0	0.67
Aristida sp.	0	0.67
Dactyloctenium aegyptium	0	0.67
Trichoneura grandiglumis	0	0.67
Brachiaria deflexa	0	0.67
Tragus berteronianus	0	0.67
Enneapogon scoparius	0	1.35
Chloris virgata	0	1.35
Sporobolus ioclados	0	2.08
Eragrostis chloromelas	0	2.08
Tricholaena monachne	0	2.69
Eragrostis cilianensis	0	2.75
Cymbopogon excavatus	0	2.75
Pogonarthria squarrosa	0.01	5.50
Setaria sp.	0.03	5.86
Eragrostis trichophora	0.03	6.53
Bothriochloa insculpta	0.02	6.78
Enneapogon cenchroides	0.01	6.91
Aristida congesta subsp. *congesta*	0.01	7.58
Brachiaria nigropedata	0.05	8.20
Eragrostis gummiflua	0.08	9.74
Urochloa oligotricha	0.05	14.71
Aristida congesta subsp. *barbicollis*	0.04	20.20
Eragrostis rigidior	0.91	33.26
Heteropogon contortus	0.14	37.46
Setaria incrassata	0.37	40.39
Panicum maximum	0.14	54.46

Cymbopogon plurinodis	0.27	69.18
Schmidtia pappophoroides	0.86	74.78
Eragrostis superba	0.57	75.15
Urochloa mosambicensis	0.86	89.71
Panicum coloratum	0.86	111.25
Themeda triandra	1.41	113.04
Bothriochloa radicans	1.58	132.60
Digitaria eriantha	2.71	200.42
Totals:	11.01	1143.44

Community structure

Projected canopy covers for trees and dwarf shrubs were very high in comparison to both other control patches as well as feeding patches (Table 31). This inevitably results in a lower overall cover of grass due to interspecific competition. Figure 10 provides a graphical representation of the community structure.

Table 31: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	1.17%	7.84%
Shrub	0.28%	1.90%
Dwarf shrub	1.61%	10.75%
Grass	11.01%	73.59%
Forb	0.88%	5.91%
Total class cover	14.96%	

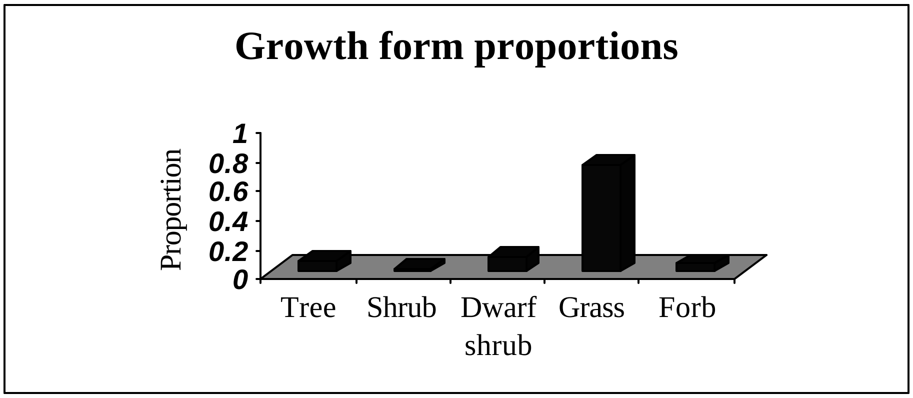


Figure 10: Histogram showing the relative proportion each growth form contributes to the community.

G. Community 2

Shrub *Euclea divinorum/Diheteropogon amplectens* Low Sparse Woodland on predominantly Gabbro and Gneiss.

The geological split of this community is 60% Gabbro/Gneiss and 40% Basalt. Due to the higher proportion of Granitic patches, this community was deemed more representative of control patches on Granite than Basalt. No definite catenal or seasonal affiliation is apparent, with Valley Bottoms positions absent (Table 32). Two well-utilised grass species feature as key species in this community, *Digitaria eriantha* and *Panicum maximum*. Due to the cross-section of catenas, key species from both upper and lower slopes are present. The community phytomass is lower than any computed for feeding patches. *Bothriochloa radicans* again features in the top four grass species in terms of biomass.

Community statistics

Total relevés in community: 15

Total species in community: 106

Total diagnostic species in community: 43

Diagnostic proportion: 40.57%

Species richness in terms of mean species per relevé: 18

Table 32: List of relevés that constitute this community and their respective catena positions and Land Type classification (Venter, 1990).

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
76	Midslope (upper)	Muzandzeni	Wet	S	South	Gneiss
67	Footslope (on midslope)	Muzandzeni	Wet	S	North-West	Gneiss
26	Midslope (lower)	Orpen	Dry	T	South	Gabbro
79	Crest	Orpen	Dry	S	North	Gabbro
39	Crest	Satara	Dry	M	West	Basalt
5	Footslope	Satara	Wet	Ma11	North	Basalt
47	Footslope	Mavumbye	Wet	Mb5	North	Basalt
46	Footslope	Mavumbye	Wet	Mb5	East	Basalt
48	Crest	Vutome	Wet	T	North	Ecca-shale
38	Midslope	Muzandzeni	Dry	T	South	Gneiss
45	Midslope	Vutome	Dry	T	East	Ecca-shale
73	Crest	Mavumbye	Wet	M	South	Basalt
4	Midslope	Satara	Wet	M	East	Basalt
14	Footslope	Orpen	Dry	T	North	Gabbro
53	Footslope	Orpen	Wet	Td1	East	Gabbro

<u>Key species</u>

Panicum maximum and *Digitaria eriantha* feature strongly in this community (Table 33), but may be mediated by the presence of *Setaria incrassata* and *Bothriochloa radicans*, as well as a high cover of forbs (2.76%).

Table 33: Key Species/Strong Competitors for each growth form class.

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
Combretum apiculatum	*Combretum apiculatum*	*Gymnosporia buxifolia*	*Digitaria eriantha*	*Vernonia* sp.
	Euclea divinorum	*Acacia exuvialis*	*Setaria incrassata*	*Cleome oxyphylla* var. *oxyphylla*
			Panicum maximum	

Dominant species

Table 34 shows *Setaria incrassata* to be of moderate biomass within the community yet has the third highest canopy cover. This high canopy cover provides the microclimate suitable for the establishment of *Panicum maximum*, but may also mask its abundance to large bodied foraging animals.

Table 34: Dominant species in community with respect to percentage canopy cover.

Species	% Canopy Cover
Panicum maximum	1.92
Digitaria eriantha	1.72
Setaria incrassata	1.11

Grass biomass

The grass biomass for this community was comparatively low, lower than that for any feeding patch community. Species contributing strongly to the community biomass, include *Bothriochloa radicans, Schmidtia pappophoroides* and *Setaria incrassata* (Table 35).

Table 35: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Sporobolus ioclados	0	1.48
Enneapogon scoparius	0	1.48
Eragrostis trichophora	0	1.48
Fingerhuthia africana	0	2.96
Tricholaena monachne	0.01	4.58
Melinis repens	0.01	4.58
Enneapogon cenchroides	0.01	6.05
Brachiaria nigropedata	0.03	8.85
Cenchrus ciliaris	0.03	8.85

Tragus berteronianus	0.06	12.89
Heteropogon contortus	0.01	13.45
Aristida congesta subsp. *barbicollis*	0.02	13.59
Cymbopogon plurinodis	0.02	15.07
Diheteropogon amplectens	0.05	17.70
Bothriochloa insculpta	0.17	22.91
Eragrostis rigidior	0.41	44.47
Eragrostis superba	0.24	44.95
Themeda triandra	0.38	54.32
Setaria incrassata	1.11	65.25
Panicum coloratum	0.63	75.61
Schmidtia pappophoroides	0.85	85.26
Bothriochloa radicans	0.74	89.25
Urochloa mosambicensis	0.63	112.05
Digitaria eriantha	1.72	122.48
Panicum maximum	1.92	131.91
Totals:	9.03	961.44

Community structure

The woody composition of this community is moderate, with a relatively high forb ratio (Figure 11). All woody growth forms are well represented (Table 36).

Table 36: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.12%	0.90%
Shrub	0.94%	7.05%
Dwarf shrub	0.46%	3.44%
Grass	9.03%	67.88%
Forb	2.76%	20.74%
Total class cover	13.30%	

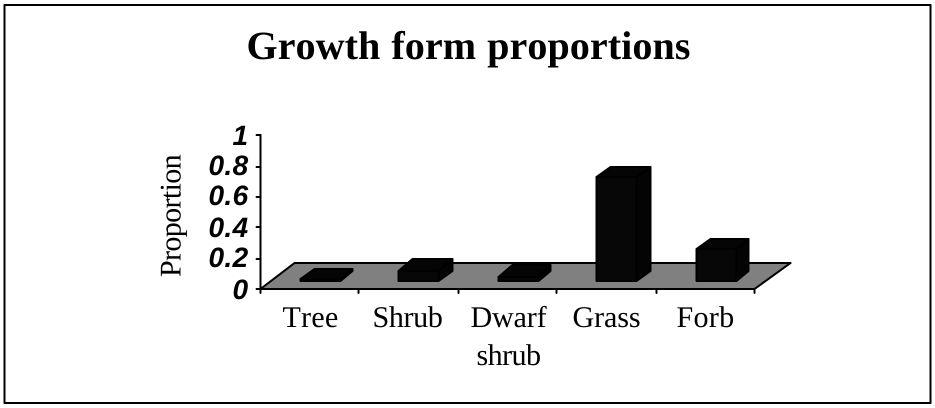


Figure 11: Histogram showing the relative proportion each growth form contributes to the community.

2.3.1.3.2 Community types on Basalt substrate

H. Community 3

Shrub *Acacia borleae/Lintonia nutans* Tall Open Shrubland on Basalt.

The twelve relevés that comprise this community are made up of predominantly the upper reaches of the basalt plains, sampled over the wet months (Table 37). Forbs contribute heavily toward the key floristics of this community in terms of projected canopy cover. The shrub proportion was the highest computed for any feeding or control community. This high shrub biomass is largely attributed to the presence of *Acacia borleae*, which grows prolifically along the footslopes and midslopes of the basalt plains, where it almost forms an impenetrable monoculture. *Bothriochloa radicans* is, as for all control communities, a prominent species, having the fourth highest grass species biomass in the community. Large trees are mostly absent from this community, which is fairly characteristic of the basalt plains, where large trees are few and dispersed. The most striking feature of the community was its very low overall biomass (810.84 kg/ha).

<u>Community statistics</u>

Total relevés in community: 12

Total species in community: 69

Total diagnostic species in community: 26

Diagnostic proportion: 37.68%

Species richness in terms of mean species per relevé: 15

Table 37: List of relevés that constitute this community and their respective catena positions and Land Type classification (Venter, 1990).

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
83	Midslope (upper)	Satara	Dry	M	West	Basalt
77	Crest	Mavumbye	Dry	M	North	Basalt
74	Crest	Mavumbye	Wet	M	East	Basalt
80	Midslope (upper)	Satara	Dry	M	North	Basalt
71	Footslope	Mavumbye	Wet	M	West	Basalt
84	Midslope	Satara	Dry	M	East	Basalt
51	Midslope	Satara	Wet	M	East	Basalt
3	Crest	Satara	Wet	M	South-West	Basalt
68	Midslope	Satara	Wet	M	South	Basalt
62	Midslope	Mavumbye	Wet	M	North	Basalt
57	Midslope	Satara	Wet	Ma17	East	Basalt
70	Crest	Satara	Wet	M	South	Basalt

Key species

Sprawling dense stands of *Acacia borleae* occur along the mid and lower reaches of this community, tracking the drainage systems. They had the highest projected canopy of any growth form or species. Their impenetrable growth form makes these areas largely unusable to herds. Several dwarf shrubs were key species (Table 38); their stunted forms largely a consequence of the prevailing soil conditions. Other than *Urochloa mosambicensis*, no other preferred species to buffalo featured.

Table 38: Key Species/Strong Competitors for each growth form class.

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
	Acacia borleae	*Gymnospora buxifolia*	*Urochloa mosambicensis*	*Heliotropicum steudneri*
		Ehretia amoena	*Lintonia nutans*	*Ceratotheca triloba*
		Barleria bleferrous		*Tephrosia* sp.

Dominant species

Acacia borleae was heavily dominant in this community (Table 39), undoubtedly acting as a strong deterrent to herds using the area, due to the thicket nature of the plant and subsequent low and inaccessible grazing below its canopy. Another deterrent may be the inhibited vigilance to predators while in the thicket, and poor visual and audible contact of individuals with one another (including cows with calves). *Themeda triandra* and *U. mosambicensis* were the two dominant grass species of this community, even though the canopy cover for *T. triandra* computed relatively low.

Table 39: Dominant species in community with respect to percentage canopy cover.

Species	% Canopy Cover
Acacia borleae (shrub)	6.72
Urochloa mosambicensis	1.84
Themeda triandra	0.97

Grass biomass

The overall phytomass for the community was well below that of feeding patches, indeed that of the other control patches too. The three most abundant species feature amongst the preferred suite of forage species to buffalo (Macandza *et al*., 2004), but *Bothriochloa radicans* again maintains a prominent fourth position in the rank of community phytomass contributors. A detailed grass species list with specific phytomass and projected canopy covers appears in Table 40.

Table 40: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Tragus berteronianus	0	1.85
Chloris virgata	0	1.85
Aristida congesta subsp. *congesta*	0	3.70
Urochloa oligotricha	0.01	5.72
Enneapogon scoparius	0.01	5.72
Aristida adscensionis	0.01	7.57
Heteropogon contortus	0.01	11.27
Digitaria eriantha	0.01	13.11
Cenchrus ciliaris	0.02	13.29
Aristida congesta subsp. *barbicollis*	0.04	18.63
Ischaemum afrum	0.13	20.69
Enneapogon cenchroides	0.21	28.64
Bothriochloa insculpta	0.3	28.80
Eragrostis superba	0.22	30.66
Lintonia nutans	0.41	32.28
Setaria incrassata	0.16	37.95
Schmidtia pappophoroides	0.13	40.46
Panicum maximum	0.34	57.22
Bothriochloa radicans	0.5	75.26
Themeda triandra	0.97	104.65
Panicum coloratum	0.67	127.16
Urochloa mosambicensis	1.84	144.39
Totals:	6	810.84

Community structure

The canopy cover of the shrubs in this community was very high (Table 41). Should predator detection and hence visibility influence patch selection, shrub density may indeed have the largest influence on site selection as they inhibit visibility at the observation height of buffalo. Almost no large trees were present and a low grass canopy cover contributed to a low overall phytomass.

Table 41: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.00%	0.01%
Shrub	6.78%	43.44%
Dwarf shrub	0.55%	3.55%
Grass	6.00%	38.42%
Forb	2.28%	14.59%
Total class cover	15.61%	

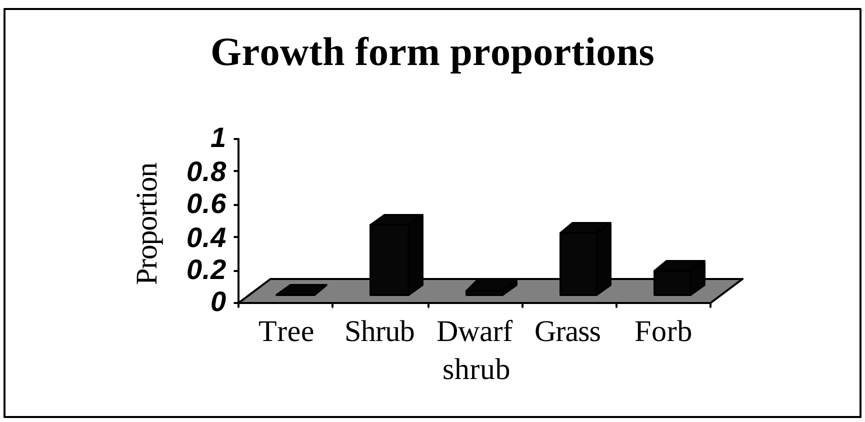


Figure 12: Histogram showing the relative proportion each growth form contributes to the community.

I. Community 4

Tree *Acacia tortillis/Sporobolus cunsimilis* Tall Sparse Woodland on Basalt.

This community predominantly represented the dry season control patches on basalt substrate. While the catenal affiliation included most sequences, the majority were made up of midslopes. Considering the majority of feeding patches in the dry season were close to water the sampling distance to control sites would generally place them into the next catena type namely, crests or midslopes. Table 42 provides a detailed breakdown of the patch landscape specifics.

<u>Community statistics</u>

Total relevés in community: 26

Total species in community: 81

Total diagnostic species in community: 20

Diagnostic proportion: 24.69%

Species richness in terms of mean species per relevé: 12

Table 42: List of relevés that constitute this community and their respective catena positions and Land Type classification (Venter, 1990).

Relevé	Catena	Land Type	Season	Herd	Aspect	Geology
8	Midslope	Mavumbye	Wet	M	West	Basalt
54	Midslope	Satara	Wet	M	South-West	Basalt
86	Midslope (lower)	Mavumbye	Dry	M	East	Basalt
44	Midslope	Satara	Dry	M	East	Basalt
85	Footslope	Mavumbye	Dry	M	South	Basalt
50	Midslope	Satara	Wet	M	West	Basalt
42	Footslope	Satara	Dry	T	North-East	Basalt
30	Midslope	Mavumbye	Dry	M	North	Basalt
60	Midslope	Satara	Wet	M	North-West	Basalt
65	Midslope (lower)	Mavumbye	Wet	Ma19	East	Basalt
32	Crest	Mavumbye	Dry	M	South-East	Basalt
24	Midslope (lower)	Mavumbye	Dry	M	South	Basalt
61	Midslope	Mavumbye	Wet	M	East	Basalt

36	Footslope	Mavumbye	Dry	M	East	Basalt
20	Footslope	Satara	Dry	M	South-East	Basalt
17	Midslope	Satara	Dry	M	West	Basalt
13	Midslope	Satara	Dry	M	North-West	Basalt
6	Footslope	Mavumbye	Wet	M	South-East	Basalt
7	Crest	Mavumbye	Wet	M	East	Basalt
12	Footslope	Mavumbye	Dry	M	South	Basalt
35	Midslope	Mavumbye	Dry	M	No data	Basalt
19	Crest	Satara	Dry	M	West	Basalt
27	Midslope (lower)	Mavumbye	Dry	M	North	Basalt
18	Footslope	Mavumbye	Dry	M	North-East	Basalt
23	Valley bottom	Mavumbye	Dry	M	South	Basalt
2	Footslope	Satara	Wet	M	North	Basalt

Key species

Combretum sp. that frequent the lower- and midslopes are key species in this community. *Combretum imberbe* particularly occurs sporadically throughout the basalt plains, standing like sentinels in a sea of grassland. *Sporobolus ioclados* and *Urochloa mosambicensis* are the two key grass species. *Vernonia* sp. were difficult to identify to species level, especially when not flowering, and were thus only identified to genus level, but undoubtedly encompasses several species. These plants were widespread on the basalt-derived soils, and can be found on both under- and over-utilised veld. The full key species list appears in Table 43.

Table 43: Key Species/Strong Competitors for each growth form class.

Trees	Shrubs	Dwarf shrubs	Grasses	Forbs
	Combretum hereroense	*Combretum imberbe*	*Sporobolus ioclados*	*Vernonia* sp.
	Combretum mossambicense	*Combretum mossambicense*	*Urochloa mosambicensis*	*Abutilon* sp.

Dominant species

Sporobolus ioclados is both a key and dominant species of this community. *Urochloa mosambicensis* and *Panicum coloratum* are also dominant grasses, often occurring together within a stand of vegetation. They both dominate in open veld where conditions are too hot and exposed for other more moisture sensitive species. Table 44 provides the percentage canopy cover for each dominant species.

Table 44: Dominant species in community with respect to percentage canopy cover.

Species	% Canopy Cover
Sporobolus ioclados	3.91
Urochloa mosambicensis	2.38
Panicum coloratum	2.15

Grass biomass

The midslopes traditionally have lower soil moisture and nutrients than lower down the slope, effectively acting as a retardant on net primary production, and hence lower overall phytomass. The biomass for this community was moderate with a high percentage of the biomass made up of preferred forage species (Macandza *et al*., 2004), with the exception of *Setaria incrassata* (Table 45).

Table 45: Mean community grass biomass in order of ascending abundance.

	Mean cover (%)	Mean biomass (kg/ha)
Chloris pycnothrix	0	0.85
Cynodon dactylon	0	0.85
Dyschoriste rogersii	0	0.85
Eragrostis rigidior	0	1.71
Fingerhuthia africana	0	2.56
Cyperus sp.	0	2.64
Bothriochloa insculpta	0	2.64

Aristida congesta subsp. *barbicollis*	0	3.49
Sporobolus nitens	0.06	9.55
Enneapogon scoparius	0.01	9.63
Ischaemum afrum	0.05	12.54
Heteropogon contortus	0.04	16.98
Eragrostis superba	0.11	18.32
Sporobolus cunsimilis	0.32	20.24
Enneapogon cenchroides	0.14	27.92
Schmidtia pappophoroides	0.19	28.48
Aristida adscensionis	0.21	31.66
Bothriochloa radicans	0.28	37.39
Digitaria eriantha	0.34	43.17
Themeda triandra	0.34	46.94
Cenchrus ciliaris	0.87	72.35
Sporobolus ioclados	3.91	95.74
Setaria incrassata	1.5	98.62
Panicum coloratum	2.15	129.26
Panicum maximum	1.04	130.47
Urochloa mosambicensis	2.38	161.73
Totals:	13.97	1006.59

Community structure

The herbaceous layer contributed significantly (in the non-statistical sense) to the overall canopy cover of this community (Table 46). While all woody categories are represented, they are all at moderate abundances, including forbs. Graphical representation of community structure is depicted in Figure13.

Table 46: Community structure arranged by growth form.

Growth form	Cover	Proportion
Tree	0.03%	0.18%
Shrub	0.35%	2.10%
Dwarf shrub	0.47%	2.82%
Grass	13.97%	84.62%
Forb	1.70%	10.28%
Total class cover	16.51%	

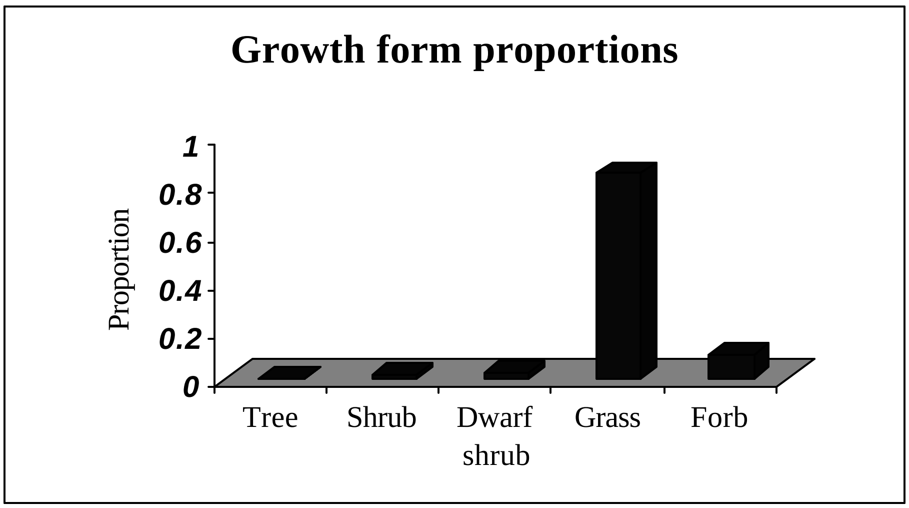


Figure 13: Histogram showing the relative proportion each growth form contributes to the community.

2.3.2 Synthesis of community variables

Table 47 shows that feeding patch communities had on average a lower woody and forb cover, a higher grass cover and a lower species diversity. The mean grass biomass for feeding patch communities was also higher than that for control patch communities.

Testing the statistical significance of these differences will be covered in the following chapter.

Table 47: Community variables of feeding and control communities. Percentage Canopy Cover is abbreviated as %CC. The values in the table below shows that feeding patches have a lower mean woody component, a higher grass proportion and higher grass phytomass. Feeding patches also have a lower species diversity than control patches.

Feeding

Community	1	2	3	4	5	Mean
Trees (%CC)	0.00	0.04	0.88	0.89	0.00	0.36
Shrubs (%CC)	0.16	0.11	0.40	1.62	0.42	0.54
Dwarf shrubs (%CC)	0.36	0.11	0.87	0.94	0.00	0.46
Total woodies (%CC)						1.36
Grasses (%CC)	15.67	12.63	7.69	13.06	24.69	14.75
Forbs (%CC)	1.36	0.24	3.01	0.63	0.02	1.05
Total cover (%CC)	17.54	13.13	12.86	17.15	25.14	17.16
Nr grass species	25	23	19	31	13	22.20
Nr plant species	85	82	80	113	21	76.20
Mean sp/relevé	14	14	23	18	5	14.80
Phytomass (kg/ha)	1033.07	1054.24	1162.726	1249.029	1048.793	1109.57

Control

Community	1	2	3	4	Mean
Trees	1.17	0.12	0.00	0.03	0.33
Shrubs	0.28	0.94	6.78	0.35	2.0875
Dwarf shrubs	1.62	0.46	0.55	0.47	0.775
Total woodies					3.1925
Grasses	11.01	9.03	6.00	13.97	10.0025
Forbs	0.87	2.76	2.28	1.70	1.9025
Total cover	14.96	13.30	15.61	16.51	15.095
Nr grass sp.	36	25	22	26	27.25
Nr species	127	106	69	81	95.75
Mean sp/relevé	19	18	15	12	16
Phytomass	1143.444	961.44	810.844	1006.588	980.579

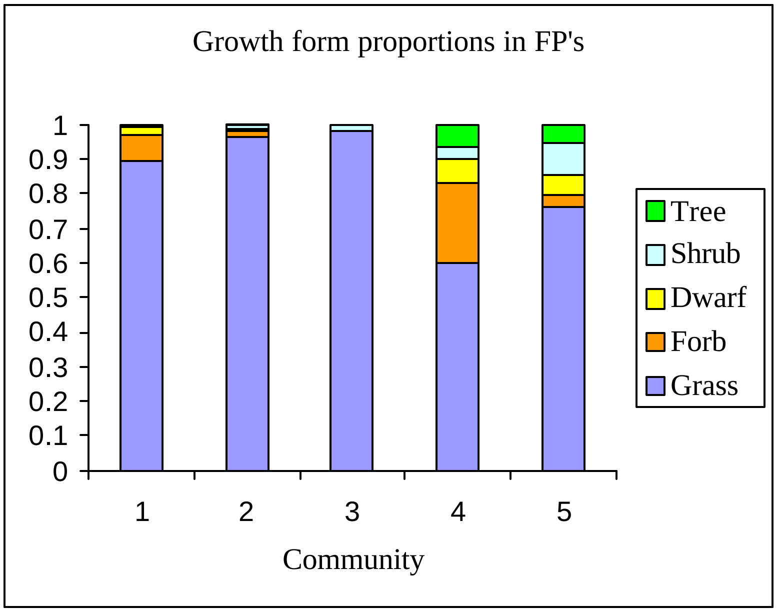


Figure 14: Graph showing the relative proportion of growth forms occurring in feeding patches (FP's). Communities 1, 2 and 3 were on Basalt substrate, while communities 4 and 5 were on Granite substrate. The feeding patches exhibit a relatively high proportion of grasses.

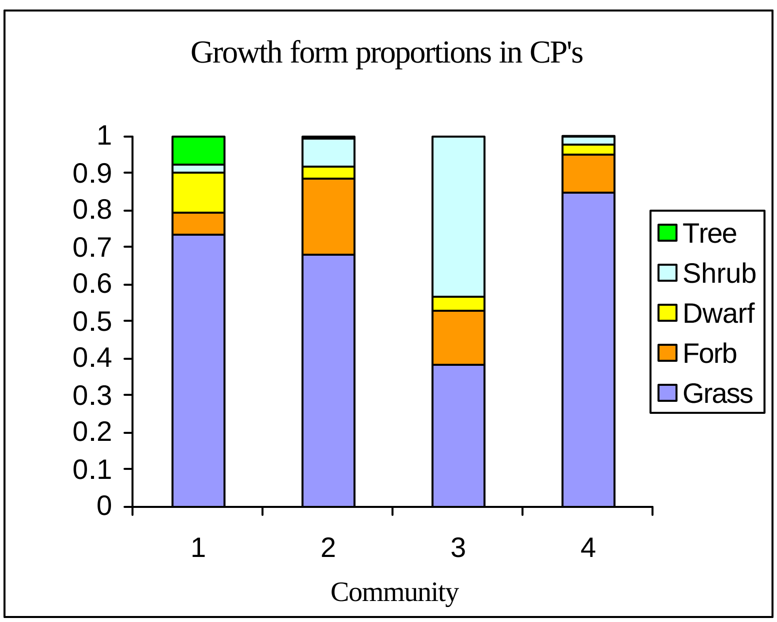


Figure 15: Graph showing the relative proportion of growth forms occurring in control patches (CP's). Communities 3 and 4 were on Basalt substrate and communities 1 and 2 on Granite substrate. Control patches show a relatively higher proportion of woody plants than feeding patches.

2.4 Discussion

It might be expected that similar floristics occur between patches occurring close to one another. The differentiating factor between feeding and control treatments seems to be the abundance of the species within each.

Patches with a high density of unpalatable species requires more search time to find preferred species' within the species matrix. Optimal foraging predicts that animals will opt for a feeding environment in which they obtain a net gain in energy (Brewer, 1994). The critical factor then becomes not necessarily what the overall phytomass is of the patch, but rather the available phytomass of palatable species.

Despite the prevalence of less preferred species holding key positions in some community types, the buffalo's selection of habitats can be largely attributed to the abundance of preferred species. The strong occurrence of less preferred species in some feeding patches is linked largely to the proximity to water of these patches (where over-utilisation by water-dependent species results in abundance of less palatable species) – buffalo often feed in close proximity to water due to their dependence on this resource.

Available grass phytomass is an essential forage requirement for a bulk-feeder. Buffalo may have a limited ability to select for specific plant parts year round. Sinclair ((1977) demonstrated how buffalo selection of the leaf fraction decreased during the dry season. Buffalo may be able to circumnavigate this problem by selecting specific species that are more palatable in spite of possible physical deterrents such as high steminess (See Appendix 3 for grass species acceptance percentages dealt with in Chapter 5).

The strong presence of the largely avoided *Setaria incrassata* in the communities occurring on the Basalt-derived soils is due to its broad-scale association with this soil type. *Setaria* also provides a micro-climate under which shade-tolerant species like *Panicum maximum* can grow, and where the two species occurred in the same patch, the buffalo would select out the *Panicum* tufts from amongst the mosaic of *Setaria* tufts.

Urochloa mosambicensis is among the preferred species in the buffalo's diet (Macandza *et al*., 2004) and due to its abundance in over-utilised areas, it supplied buffalo with suitable forage in these areas, particularly close to water sources.

Cenchrus ciliaris is a well sought after resource throughout the late dry season (Macandza *et al*., 2004), as it retains a relatively high degree of greenness. *C. ciliaris* tends to occur in sprawling stands where it dominates spatially over a localised area. These stands are often along footslopes below stands of large trees, where it can retain more moisture, due to lower heat stress and evapo-transpiration, making it more palatable than other available species over the dry season.

Sporobolus cunsimilis did not occur in many feeding patches, and due to its tall stemmy nature is unlikely to be a favoured forage species as a mature plant but the buffalo may instead choose to feed on smaller, establishing tillers.

The grass with third highest biomass in feeding patches namely, *Panicum maximum*, a shade-tolerant species, also tends to be greener than surrounding species over the dry season. In the shade of the larger trees an appropriate climate is provided in which certain species of grass can thrive and provide high quality forage to grazers throughout the year. The high canopy affords the herds protection from the elements during the hottest periods of the day. The high grass proportion provides a critical mass of quality forage, allowing herds to optimise on forage intake, with minimum energy expenditure.

Sporobolus ioclados tends to occur on well-utilised footslopes, where it forms a homogenous stand. While the tufts may be close to the ground, below the average grazing height of buffalo, they have a high leaf proportion.

The ability of *Digitaria eriantha* to produce grazing lawn type conditions coupled with a low stem proportion is likely to be among the species' strongest attractants to buffalo.

2.5 Summary and Conclusions

The fact that 73% of the patches did not occur in the same community as their control site shows that even at that fine sampling scale a large enough difference in species composition/structure exists to place them into separate plant communities and also affect the selection of patches by herds. One might surmise by saying the feeding patches have a preferential ratio of resources and hence are utilized preferentially over the bordering patch. However, once this patch has been utilized or over dry or resource limited periods herds may return to the previously avoided areas which may not have the same ratio of key resources as the preferred patch, but components of it.

The year's 2002 and 2003 experienced below average rainfall, with a clear delineation of rainfall into seasons difficult and possibly arbitrary, hence very little emphasis was placed on seasonal differences in patch selection.

Buffalo selected feeding patches that always contained an abundance of at least one of their preferred forage species. *Urochloa mosambicensis* was shown to be both a dominant and key species in the majority of feeding patches, implying its abundance to be an important contributor to patch selection by buffalo herds across both dominant geological substrates. Other species that also held key positions in many of the patches were *Sporobolus ioclados*, *Digitaria eriantha* and *Cenchrus ciliaris*. With the exception of *S. ioclados* the other three species were also those grasses ranked highly as forage species (Macandza *et al*., 2004); leading to the conclusion that buffalo forage selection is by and large determined by the local abundance of preferred grass species. Buffalo tended to feed on patches where the woody plants were present at moderate to low abundance with only a few patches having a woody species classified as dominant. Shrubs and dwarf shrubs were more abundant than large trees, with these growth forms often creating shaded areas conducive to the establishment of *P. maximum*, a well-utilised grass by buffalo throughout the year.

The feeding patch plant communities were generally separated into patches that shared a common landscape attribute, such as geomorphological unit, aspect, soil type (Land Type), season or a combination of these factors.

The mean grass biomass (phytomass) for all feeding patch communities was 1109.57 kg/ha with a range from 1033.07 kg/ha to 1249.034kg/ha. The higher biomass patches were counter-intuitively largely on the western side of the study area including Gabbro, Gneiss and Ecca shale substrates where one would assume the higher standing crop to occur on the Basalt derived soils.

A number of grass species that were key species in feeding patches were also key species in control patches namely, *Digitaria eriantha* and *Urochloa mosambicensis*. Several less palatable species were also dominant members of control patches including *Bothriochloa radicans* and *Setaria incrassata.* Control patches also had on average a lower grass biomass - 980.58 kg/ha – with a range from 810.84 kg/ha to 1143.44 kg/ha.

The overriding pattern that emerged was that feeding patches were slightly floristically distinct from neighbouring control patches and contained a higher proportion of preferred grass species, due to lower patch species diversity. The overall patch biomass was higher in feeding patches, as well as having a lower cover of woody plants.

3 Chapter 3: Quantifying the key resources responsible for patch selection

3.1 Introduction

To enable one to gain an insight into buffalo patch selection and preferences one has to gain a handle on what are the key resources that determine buffalo patch selection. Naturally, it is not possible to measure every component of a patch, however, knowing that buffalo fall into the group of bulk-feeders, deductions can be made as to what may be important variables contributing to the selection process. These variables may be both patch dependent (e.g. species composition, vegetation structure) and independent (distance to nearest drinking water).

3.2 Materials and methods for Pair-wise analysis

3.2.1 Grass phytomass

The software program-Stocking Density-which uses the same logarithms as Phytotab-PC and is supplied as part of the Phytotab-PC package, (available from Dr Bobby Westfall, ARC - Range and Forage Institute, Private Bag X05, Lynn East, 0039) was used to determine the output values for phytomass, spacing, percentage canopy cover and density, on a species-specific basis. Phytotab is designed to derive values at the community level, meaning that within a crown diameter class it uses the mean value of that class to determine the output variables. The Stocking Density application allows one to enter the actual crown diameter value for that species and not use the mean of the class (see Heading 5.2.2 -Technique for vegetation sampling - for detailed description). However, as the crown diameter class was used during the collection of field data, and not the actual crown measurement, the mean value for the class had to be used, as would be used for Phytotab-PC.

The following is an overview of the formulae used by the packages after Westfall (1998):

Percentage canopy cover, the derived variable, and mean crown diameter, the measured variable, enable plant density to be calculated as follows:

$$A = C \times 10\ 000/100$$

Where,

A = area (m2) covered by canopy in 1 ha

C = projected canopy cover of plant species, as a percentage, and

$$D = A/\pi r^2$$

Where,

D = density in terms of individuals per hectare

r = crown radius, being half mean crown diameter (m).

From this it can be concluded that given any two of the variables, cover, mean crown diameter and density, the third variable can be calculated.

The individual species scores of the respective categories (Phytomass, density etc.) for each patch were averaged to obtain a mean value for that patch.

3.2.2 Percentage moisture content

Eight grass tufts for each species were harvested at a height of 10cm above ground level for all feeding and control sites. Use of eight samples aimed to improve accuracy, as moisture content is highly variable even at fine-scales, with tufts in shade maintaining higher moisture content than those in full sun. Figure 16 shows the relationship between grass moisture content and the number of samples needed to approach an accurate mean, by using a running average of moisture content. 10cm was chosen as the harvesting height to ensure consistency in sampling as well as the corresponding unlikely selection of buffalo for very short tufts. This was shown in the results for mean grass height of the feeding patches that revealed a high occurrence of ankle to knee high tufts occurring in feeding patches. Due to financial constraints a maximum of four grass species were harvested per patch, the criteria for selection being:

a) those species utilised by the buffalo or,

b) those species in relatively high abundance in the patch, i.e. those that were allocated any symbol larger than a “1”in the variable belt transect of the Plant Number Scale.

The wet mass is recorded before being dried in an oven at 65°C for 34-36 hours. The dry matter is then weighed, and by means of a formula the moisture content is determined for each species (Trollope & Potgieter, 1986).
The individual species data were then averaged to obtain a mean for each relevé or patch, as well as a weighted average being determined by multiplying the species moisture content by the percentage phytomass that individual species contributed to the overall phytomass of the patch.

As access to a convection drying oven was difficult, and humid and hot conditions prevail over the summer months, a number of the grass samples moulded within 24-48hrs after sampling, before being dried, and had to be discarded. This reduced the original number of patches (86) that could be analysed to 66 feeding and 66 control sites.

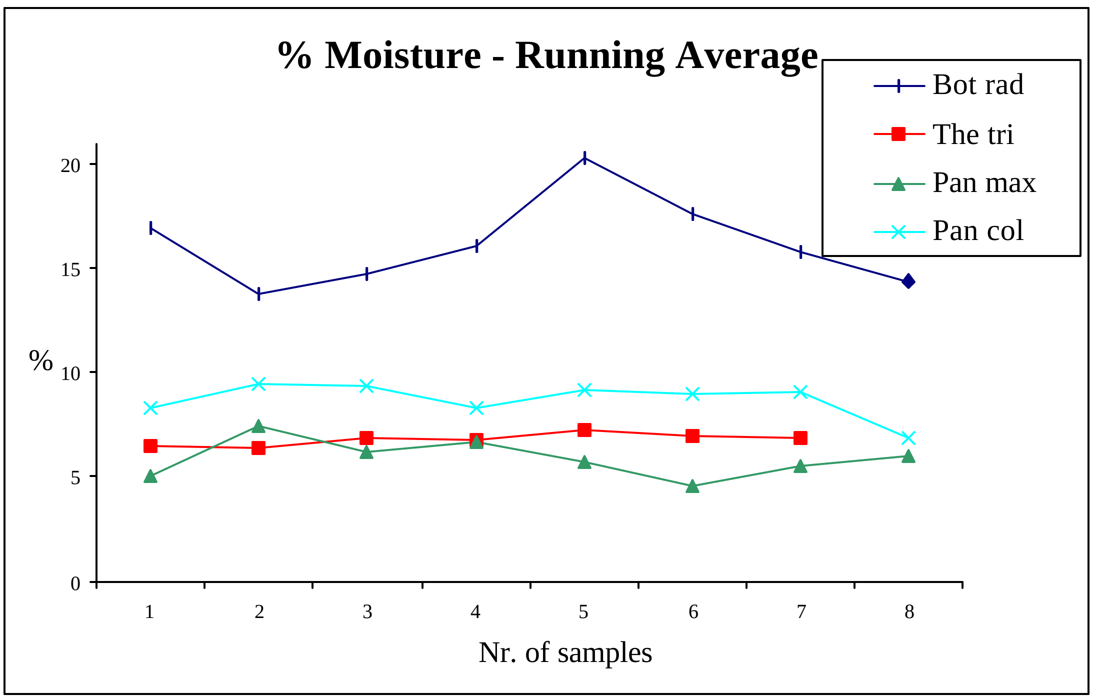


Figure 16: Running average of percentage moisture versus number of samples of four common grass species. Key to graph legend: “Bot rad” – *Botriochloa radicans*, “The tri” – *Themeda triandra*, “Pan max” – *Panicum maximum*, “ Pan col” – *Panicum coloratum*.

3.2.3 Leaf to stem ratio

The dried grass tufts were hand sorted into its component stems and leaves. The leaf and stem fractions were weighed and the stem to leaf ratio expressed on a dry mass basis. The ratio was expressed as the proportion stems in the tuft.

The stem to leaf ratios of the individual species were averaged across the patch to obtain a mean value, as well as a weighted average by the same method described under percentage moisture content (see Heading 6.2.2.). For the same reasons stated for percentage moisture content only 66 samples were available for analysis.

3.2.4 Percentage Nitrogen and Phosphorus

Percentage Nitrogen (%N) and Percentage Phosphorus (%P) of leaf matter were determined for the grass species harvested from each patch. Phosphorus and Nitrogen concentration was determined using the standard Kjeldahl technique (AOAC, 1975) by the Institute for Tropical and Sub-Tropical Crops (ITSC), a division of the Agricultural Research Council (ARC) in Nelspruit. Broadly stated the technique involves the digestion of the leaf matter and subsequent extraction of the Nitrogen and Phosphorus content.

The wet digestion for %P determination is done using a 2:1 ratio of 55% Nitric Acid and 70% Perchloric Acid.

For the digestion of plant material for percentage Nitrogen determination, the sample is digested with 4ml of 98% Sulphuric Acid and 1ml of 30% Hydrogen Peroxide.

The method of detection for Phosphorus and Nitrogen is as follows:

<u>Phosphorus</u>

Colorimetric by Auto Analyser. The determination of phosphorus is based on the colorimetric method in which a blue colour is formed by the reaction of ortho phosphate and the molybdate ion. The phosphomolybdenum complex is read at 660nm.

<u>Nitrogen</u>

Colorimetric by Auto Analyser. The determination of nitrogen is based on a colorimetric method in which an emerald-green colour is formed by the reaction of ammonia, sodium salicylate, sodium nitroprusside and sodium hypochlorite. The ammonia-salicylate complex is read at 640nm.

The individual Nitrogen and Phosphorus scores for each species were averaged for each patch to obtain the mean, as well as the weighted average. 66 samples were used for the analysis.

3.2.5 Grass to forb ratio

Using the density estimates calculated by the Stocking Density program the grass: forb ratio was expresses as a proportion of grass to forbs in the patch. This eliminated the problem when using percentage expressions, as a zero value for forb density in any patch would result in a zero denominator, which cannot be computed.

3.2.6 Distance to water

The location of the closest surface water to the patches was recorded and the distance between them determined using a Magellan GPS (Geographic Position System) set to WGS84 datum. If no apparent water existed in the vicinity of the patch, Arcview© 3.2a computer software was used to determine the closest known water source. These data were made available by the fact that all pans and water points were recorded daily on an *ad hoc* basis by field staff, throughout the herd's home ranges.

Their positions were recorded on a GPS and stored in a database to gain a more spatio-temporally refined GIS of water availability in the area.

3.2.7 Horizontal visibility

Maximum horizontal visibility was determined by taking four readings with a Bushnell Yardage Pro 500 laser rangefinder. A reading was taken in all four cardinal directions, until a "wall-effect" was evident. For areas where this effect was not clearly evident, an assistant would walk in each cardinal direction away from the observer, until visibility at 1.5m in height was lost. The readings were then averaged to gain a mean visibility value for the patch after De Wet (1988).

3.2.8 Woody density

Sampling the woody component of the patch involved classifying all present species into any of the following three categories, with a species often being present in multiple growth form categories: Dwarf Shrubs, Shrubs and Trees. The density of the combined category, that amalgamated all classes into one generic total woody class, was compared between feeding and control sites. The density estimates were all calculated using the previously mentioned "Stocking Density" program.

3.2.8.1 Statistical analysis

As a paired sampling strategy was employed a pair-wise analysis was needed to optimise the statistical power of such a sampling strategy; which allows for detection of finer-scale differences between the experimental and control. The non-parametric Sign Test in Statistica ver. 6.1 (StatSoft, Inc., 2004) was used to test for a significant difference between the feeding and control patches for all above-mentioned variables. While transformation could normalise the data, a paired design did not meet the requirements for independence. This test obviated the need for normally distributed and independent data. The only assumption required by this test is that the underlying distribution of the variable of interest is continuous; no assumptions about the nature or shape of the underlying distribution are required. The test simply computes the number of times (across subjects) that the value of the first variable (A) is larger than that of the second variable (B). Under the null hypothesis (stating that the two variables are not different from each other) we expect this to be the case about 50% of the time. Based on the binomial distribution we can compute a z value for the observed number of cases where $A > B$, and compute the associated tail probability for that z value (StatSoft, Inc., 2004).

3.3 Materials and methods for non-paired data

3.3.1 Grass height preference

The mean grass height for the patch was measured following De Wet (1988). The plant number scale takes cognisance of the diversity and canopy cover of the graminoids, but no actual measurement for grass height is recorded. This aspect may relate to feeding budgets, interspecific competition and visibility while feeding.

Six height classes were used:

- No grass.
- 120mm (ankle height).
- 500mm (knee height).
- 1000mm (waist height).
- 1500mm (shoulder height).
- Above 1500mm.

Grass height at 20 points was recorded to gain a more precise mean for the site. At each point the grass was placed into one of the six above-mentioned classes. A pilot study done during the developmental stages of the project showed that very little improvement in accuracy is gained after 12 points (Figure 17).

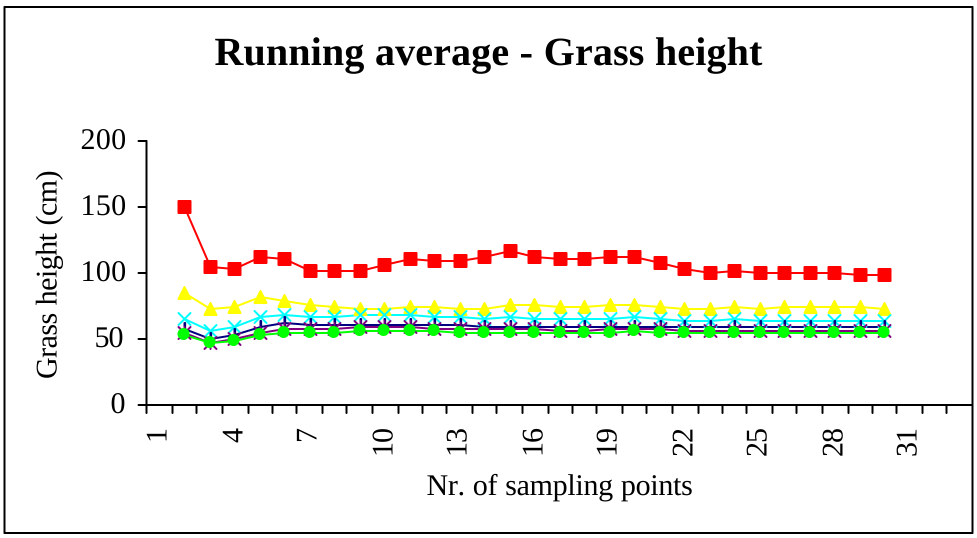


Figure 17: Running average of grass height versus number of sampling points of six patches. The graph indicates that very little improvement in the estimation of mean grass height for the patch is obtained with more than 10 sampling points.

3.3.1.1 Statistical analysis

Spearman rank correlation (Spearman R) was used in Statistica ver. 6 (StatSoft, Inc., 2004) to test the correlation in grass height categories between feeding and control patches. The test can be thought of as the regular Pearson product moment correlation coefficient (Pearson r); that is, in terms of the proportion of variability accounted for, except that Spearman R is computed from ranks. Spearman R assumes that the variables under consideration were measured on at least an ordinal (rank order) scale; that is, the individual observations (cases) can be ranked into two ordered series.

3.3.2 Geomorphological unit or community type

Each sample site was placed into one of the following subjective catenal categories (after Kruger, 1972):

- Crest.
- Midslope.
- Footslope.
- Riparian or Valley Bottom.

Grazing ungulates in African savannas concentrate their feeding in zones that shift up and down the catenary drainage gradient through the seasonal cycle, moving progressively downslope in the dry season as availability of green grass declines and then switching back to short, nutritious swards on the uplands when the rains commence (du Toit, 2003). The data collected under this heading cannot definitively test the above statement due to the sampling design and analysis used. Instead it attempts to test whether feeding patches occurred on certain catena's more than the control patches between the two measured seasons.

3.3.2.1 Statistical analysis

A chi-square test of association was used to test whether buffalo significantly associated with a particular catena or community type over the two seasons.

3.3.3 Aspect

The aspect of the slope was recorded at all sites using a compass. The discrete values were then placed into their nearest cardinal position category. The eight cardinal positions used were: N (north), NE (north-east), E (east), SE (south-east), S (south), SW (south-west), W (west), NW (north-west).

3.3.3.1 Statistical analysis

A chi-square test for association was to be used to determine if the herds showed seasonal aspect preferences. However, as more than 20% of the categories had expected frequencies of less than five (Agresti, 1990, 1996) the seasonal differentiation had to be forsaken, and observations were combined into only feeding and control observations incorporating the whole study period. Another underlying assumption of the chi-square test is that observations are classified into categories independently. While in this study, the control site is always coupled to the feeding site by a set distance; the independence criterion is only partially met. I felt that the distance between them was adequate to ensure that the location of control site did not mean it necessarily shared the same aspect, nor was it guaranteed to fall into the next category in the hillslope sequence (especially on short hillslopes, such as those on the granites).

As the aspect for one site was not taken the sample size for this analysis was 170, namely 85 feeding and 85 control sites.

3.3.4 Slope

A modified protractor was used to determine the slope as a simplified form of a clinometer. This was done by attaching a piece of string to the base of the protractor, which has a small lead weight at the loose end, along the 90° mark. The flat side was then rotated until it was subjectively parallel to the angle of the ground; the degrees were read off the protractor, which in turn was subtracted from 90 to obtain the slope.

3.3.4.1 Statistical analysis

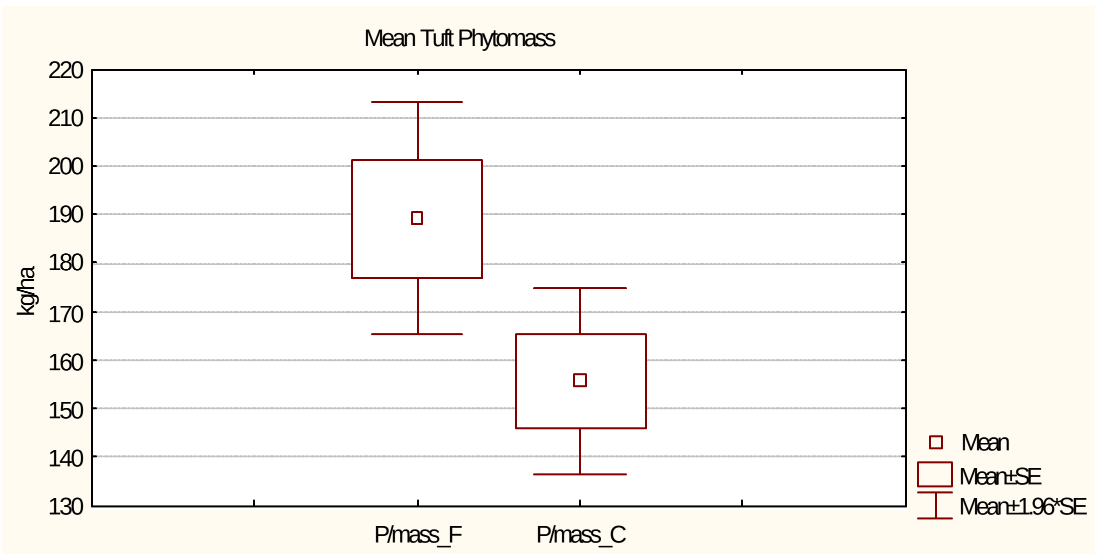
A chi-square test of association was used to determine if buffalo herds showed a preference for certain slopes over the two seasons.

3.4 Results and discussion: Pair-wise analysis

3.4.1 Mean grass tuft phytomass

A highly significant result was obtained when mean tuft phytomass was tested between feeding and control patches (Figure 18). Individual grass tufts in the feeding patches were on average much higher in biomass or phytomass than their neighbouring control patches. As buffalo are broadly classified as bulk-feeders this result would certainly be expected to be an overriding criterion for feeding patch selection.

Mean tuft phytomass varied between 57.2kg/ha to 690.1kg/ha in feeding sites and 39.6kg/ha to 718.71kg/ha in control sites.

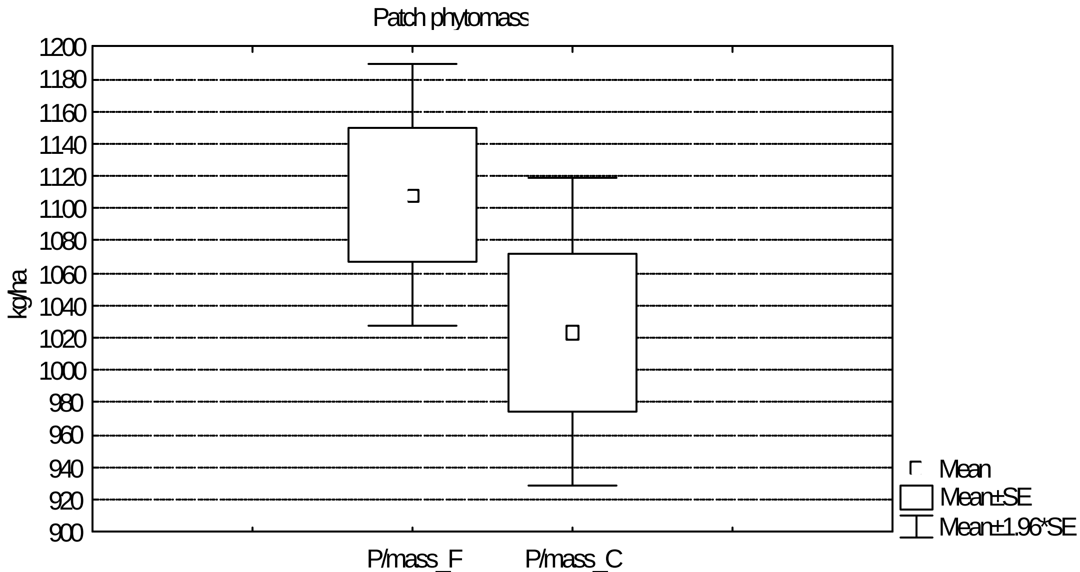


Sign test Z = 3.343, p = 0.00

Figure 18: Box and Whisker Plot: Mean tuft phytomass of feeding and control patches. Mean grass tuft phytomass is significantly higher in feeding patches than their paired control patches.

3.4.2 Total patch phytomass

As would be expected the total standing crop in feeding patches was significantly higher than in control sites (Figure 19). Hence, absolute abundance of available forage is a key resource to buffalo and a determinant of patch selection. This would support the theory that herds are capable of evaluating the standing crop differences between two neighbouring patches, and choose to feed in the one offering a higher yield.

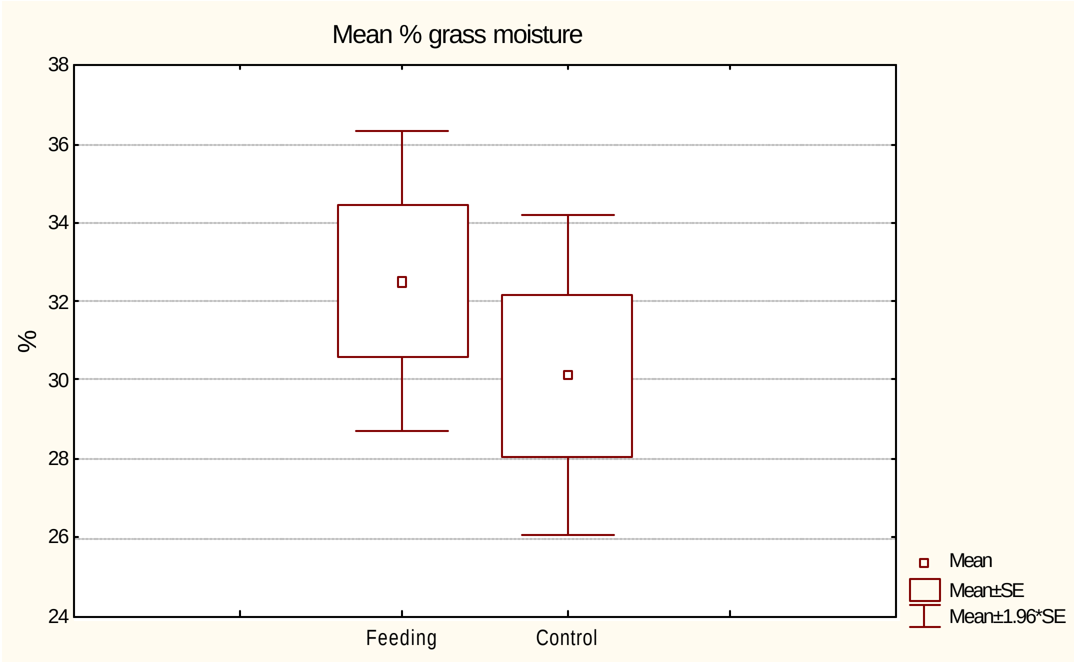


Sign test Z = 2.04, p = 0.04

Figure 19: Box and Whisker Plot: Total patch standing crop. The total standing crop (as opposed to the mean tuft phytomass in Figure 18) is significantly higher in feeding patches.

3.4.3 Mean percentage grass moisture content

A non-significant result was computed when testing mean percentage grass moisture content between feeding and control sites (Figure 20). Feeding patches did none the less have higher grass moisture content, indicating that on average, tufts in feeding patches had higher moisture content than their controls. Moisture content is highly variable – and varied through the year from as low as 0.86% to a high of 82.22% across all species - even within a localised area and may have attributed in part to the non-significant result being computed. Tufts occurring under trees, especially on their southern sides may be considerably greener than those in an open area where they will experience higher heat stress. Grass greenness may in fact play a more important role at the finer feeding station scale, where tuft selection takes place, and may not directly influence patch selection *per se*.

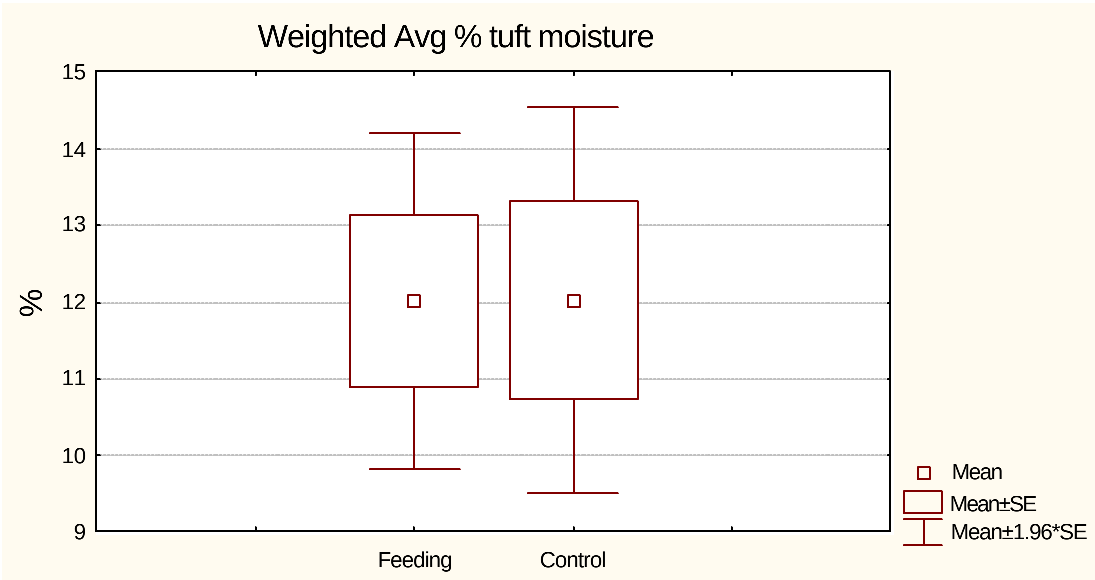


Sign test Z = 1.491202, p = 0.14

Figure 20: Box and Whisker Plot: Mean percentage grass moisture content. Mean grass tuft percentage moisture content in feeding patches is non-significantly higher than the tufts in control patches.

3.4.4 Total patch percentage grass moisture content (weighted average)

Almost no difference is seen in percentage moisture content when a weighted average is used based on the abundance (phytomass) estimates for each species, producing a non-significant result (Figure 21). This shows that the "total" or "gross" % moisture content available to the herds at feeding and control patches is nearly the same. These results may be misleading as buffalo are unlikely to have the ability to make a quantifiable assessment of the total moisture content (grass greenness being the indicator) contained in two neighbouring sites, as they for one lack the height advantage necessary to make such an assessment. It may be that grass moisture content is actually more relevant to a finer foraging scale, namely the plant bite. Hence, buffalo will not be able to judge two similarly green patches apart, based on a larger-scale greenness index but rather may select out the tufts while feeding that retain more green leaves, especially over the dry season.



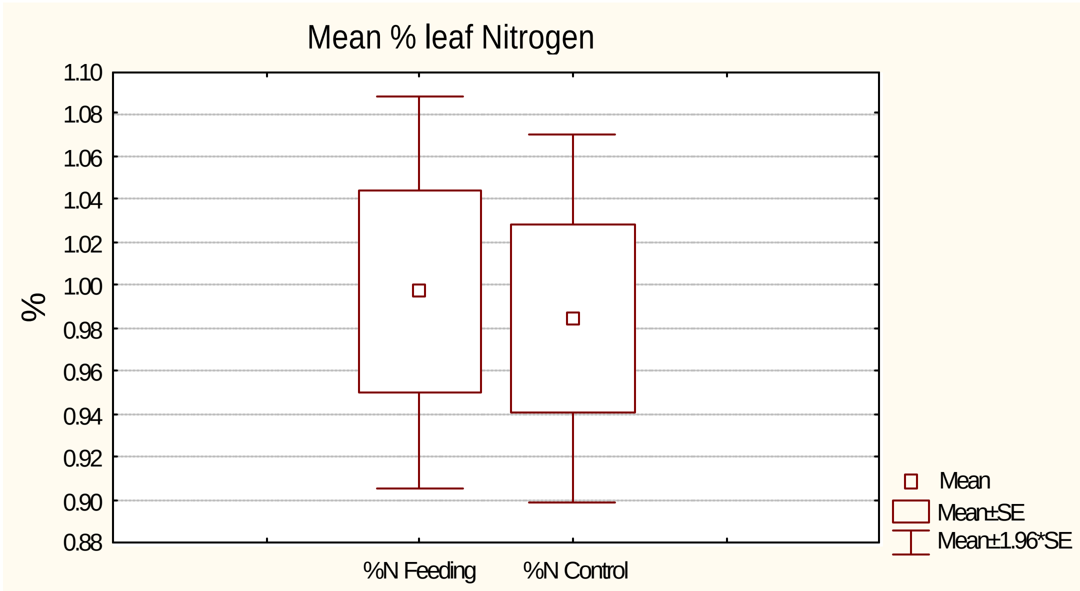
Sign test Z = 0.114708, p = 0.91

Figure 21: Box and Whisker Plot: Weighted average percentage grass moisture content. No difference in moisture content is seen between feeding and control patches, when a species' moisture content is weighted by its biomass for that patch.

3.4.5 Mean percentage leaf nitrogen content

The difference in mean percentage nitrogen in the leaves of feeding and control site tufts was negligible and non-significant, with feeding patches having only a slightly higher percentage Nitrogen (Figure 22). This result would be expected, as a fairly strong correlation exists between grass moisture content and percentage Nitrogen in leaf matter; and as was previously shown feeding patches had slightly higher mean grass moisture content than control sites did.

Tuft percentage Nitrogen for feeding patches ranged between 0.49%and 2.99% over the wet season and 0.25% and 1.43% over the dry season. Control patch tufts ranged from 0.5%to 2.66% over the wet months and 0.32 and 1.79% over the dry months.

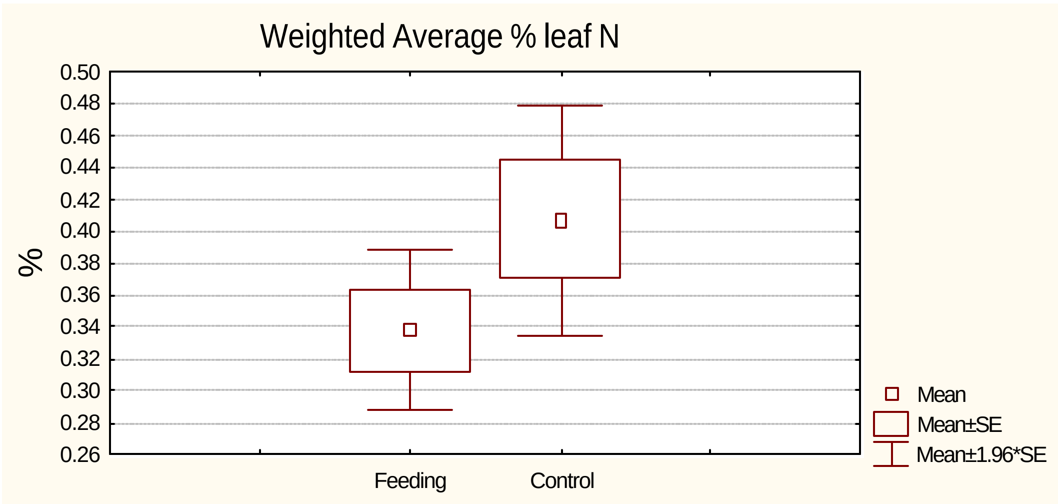


Sign test Z = 0.836660, p = 0.40

Figure 22: Box and Whisker Plot: Mean percentage leaf Nitrogen content. Feeding patches computed non-significantly higher percentage leaf Nitrogen content than control patches.

3.4.6 Total patch percentage leaf Nitrogen content (weighted average)

Weighted average percentage Nitrogen shows a different relationship to that of the mean percentage Nitrogen, whereby the control sites had a non-significantly higher gross nitrogen content (Figure 23). This is once again a scale-related issue, whereby buffalo cannot ascertain the different total percentage Nitrogen values of neighbouring sites. Hence, the mean leaf percentage Nitrogen content is a more applicable measurement as the buffalo may only select for greener tufts (and hence higher percentage N leaves) at the feeding station scale, when they are faced with a number of options directly below their fore feet.

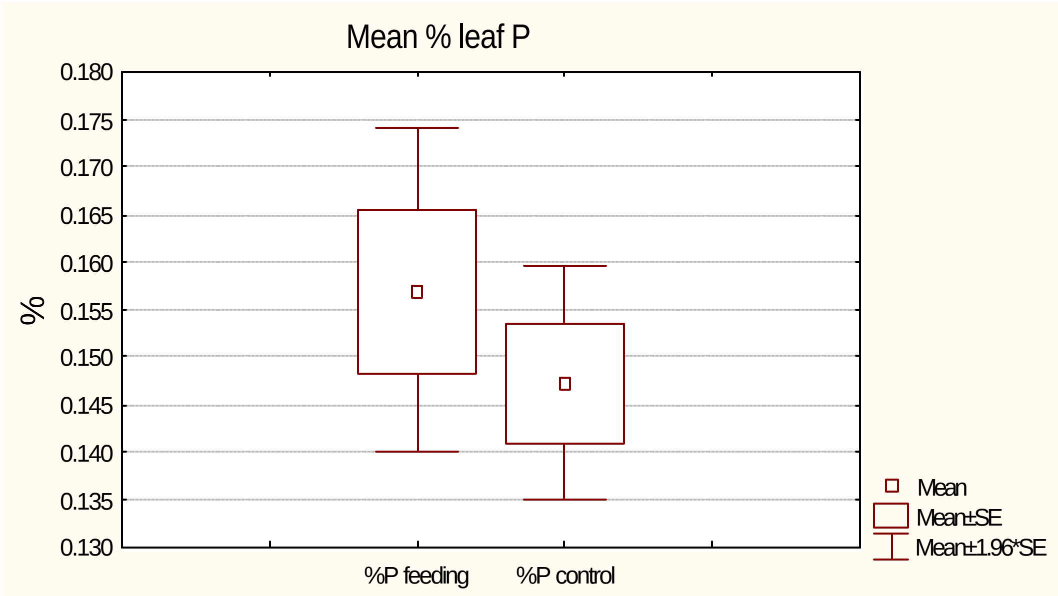


Sign test Z = 0.615457, p = 0.54

Figure 23: Box and Whisker plot: Weighted average percentage leaf nitrogen. The percentage Nitrogen grass leaf content in feeding patches was non-significantly lower than that of control grass leaf content when percentage Nitrogen is weighted by biomass.

3.4.7 Mean percentage leaf Phosphorus content

Feeding sites showed a non-significantly higher mean percentage Phosphorus content in their tuft leaves than did the control patch tufts (Figure 24). Percentage leaf Phosphorus ranged between 0.066% and 0.454% for feeding patch tufts over the wet season and 0.038% and 0.478% over the dry season. The control patch tufts ranged in percent Phosphorus between 0.086% and 0.46% over the wet season and 0.033% and 0.325% over the dry season.

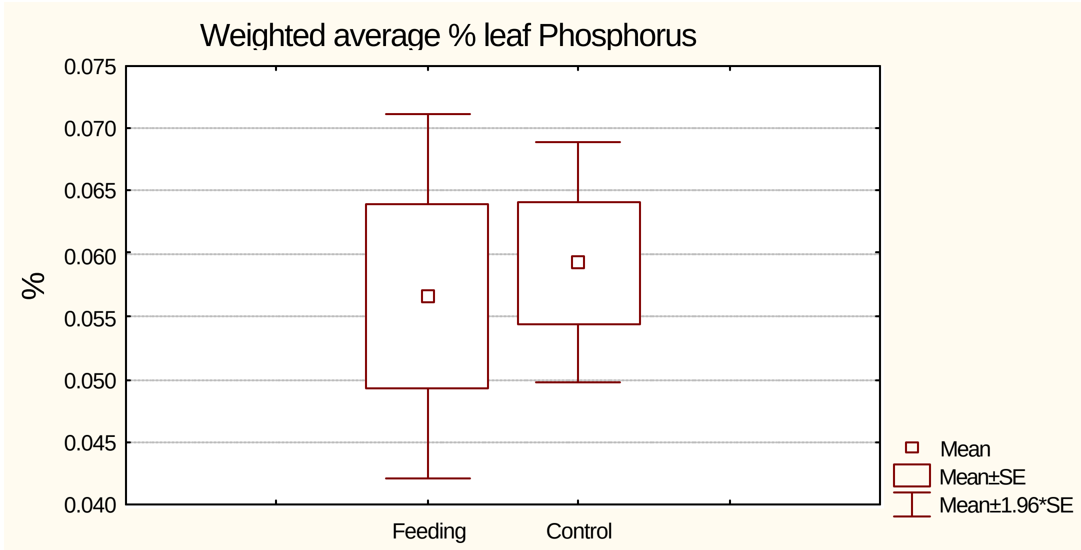


Sign test Z = 0.358569, p = 0.72

Figure 24: Box and Whisker Plot: Mean percentage leaf Phosphorus content. Grass percentage Phosphorus content was non-significantly higher in feeding patches than in control patches.

3.4.8 Total patch percentage leaf Phosphorus content (weighted average)

Control patches showed a marginally, non-significantly, higher total patch percentage leaf Phosphorus content than feeding patches (Figure 25).



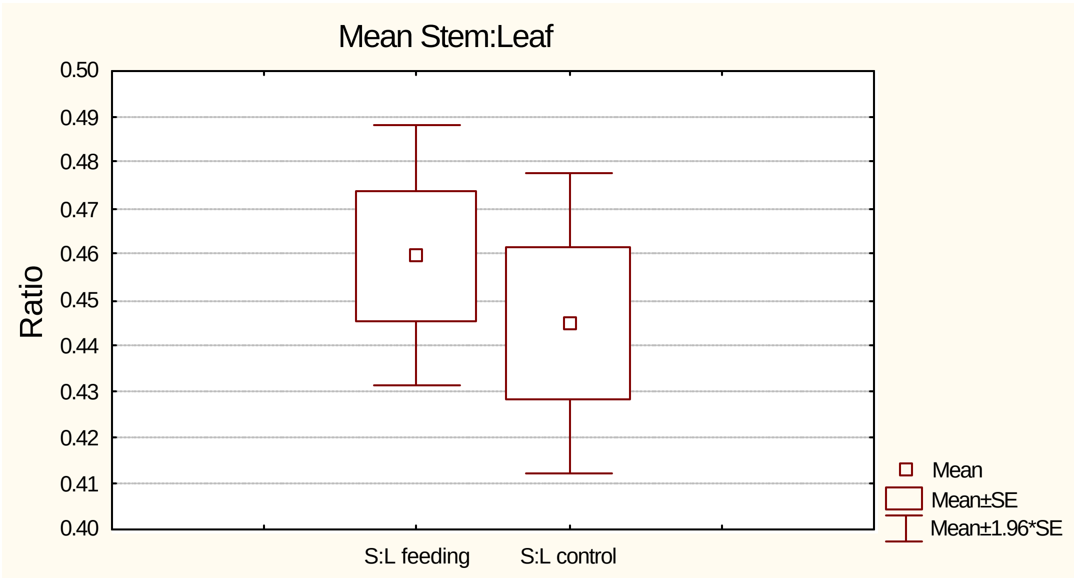
Sign test Z = 1.600189, p = 0.11

Figure 25: Box and Whisker Plot: Weighted average percentage leaf phosphorus. Grass leaves in feeding patches computed a slightly lower (non-significant) percentage Phosphorus content than those in control patches.

3.4.9 Mean stem to leaf ratio

Feeding patch tufts had a non-significantly higher stem to leaf ratio than did control patch tufts. This implies that grass tufts in feeding patches were on average higher in stem content than were those in the control sites

Tuft stem to leaf ratios ranged from 0.027 to 0.842 in the wet season and 0.019 to 0.762 in the dry season for feeding patches and from 0.061 to 0.829 in the wet season and 0.010 to 0.852 over the dry months for control patches.

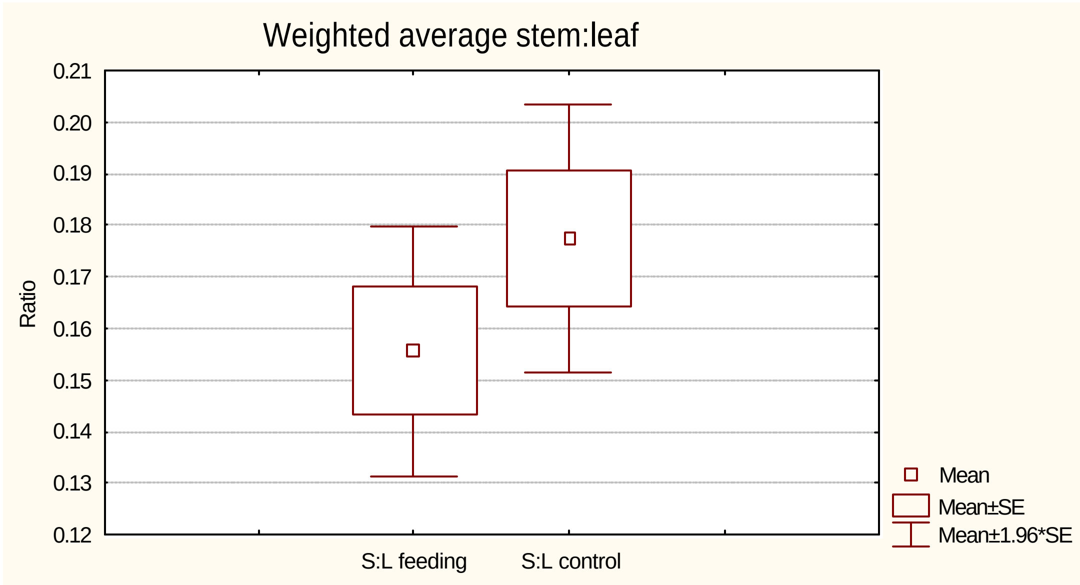


Sign test Z = -0.000, p = 1.00

Figure 26: Box and Whisker Plot: Mean stem to leaf ratio. Grass tufts in feeding patches computed a non-significantly higher stem proportion than control tufts.

3.4.10 Patch stem leaf ratio

Feeding patches showed a lower patch stem to leaf ratio than control sites (Figure 27). This difference was non-significant. It could be debated as to whether or not buffalo are able to assess a patch's average steminess and consequently differentiate one patch from another.

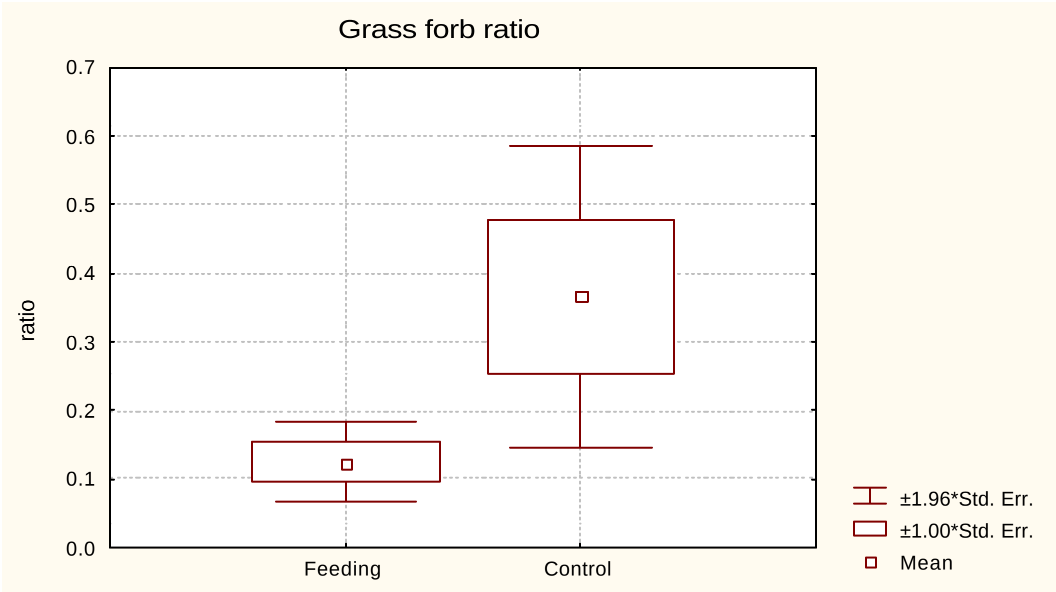


Sign test Z = 0.615457, p = 0.54

Figure 27: Box and Whisker Plot: Weighted average stem to leaf ratio (or total patch steminess). Grass tufts computed a lower stem proportion when weighted by relative abundance (biomass).

3.4.11 Grass to forb ratio

Feeding patches computed a significantly lower grass to forb ratio than control patches (Figure 28); meaning that there was a higher abundance of forbs and lower proportion of grasses in feeding patches than in control sites. This result was somewhat unexpected, as one would have expected sites that have high grass biomass to have lower forb abundance due to competitive exclusion.

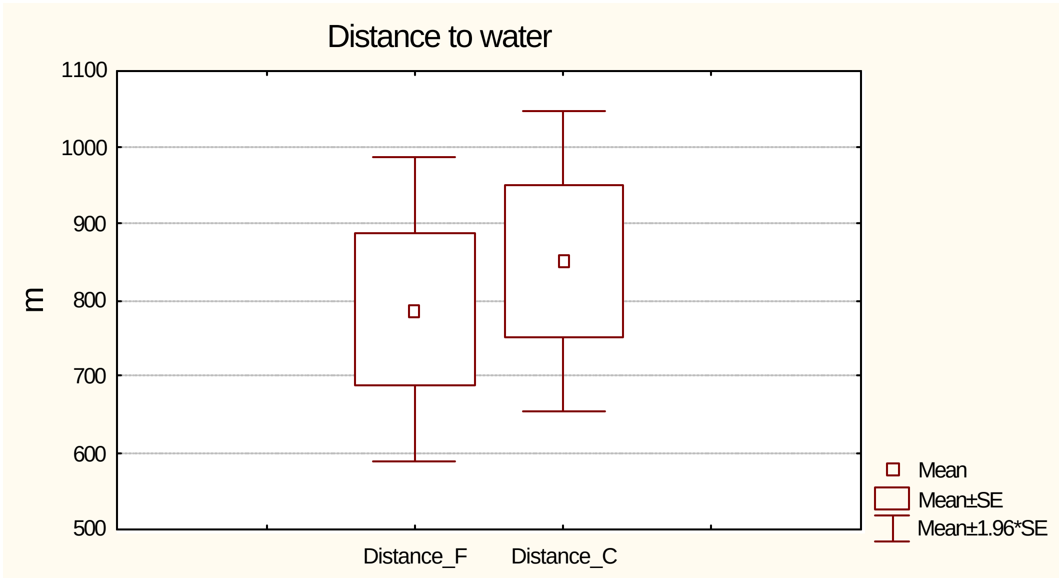


Sign test Z = 2.507133, p = 0.01

Figure 28: Box and Whisker Plot: Grass proportion of feeding and control patches. Forbs expressed themselves at a significantly higher abundance in feeding patches than in control patches.

3.4.12 Distance to closest surface drinking water

A highly significant difference between feeding patches and control sites was computed when testing the distance to closest surface water, with feeding patches being closest (Figure 29). This result was somewhat surprising as the control site was always only 100m away from the edge of the foraging path. Such a result could be easily expected were the control sites randomly distanced from the feeding patches. Buffalo are water dependent and consequently are limited in the range they may utilise by the availability of free-standing water. Feeding patches were situated between 30m and 5600m from water over the wet season and between 25m and 3600m over the dry season. Control sites ranged from between 55m and 5360m from surface water during the wet season, and between 20m and 4020m through the dry season.

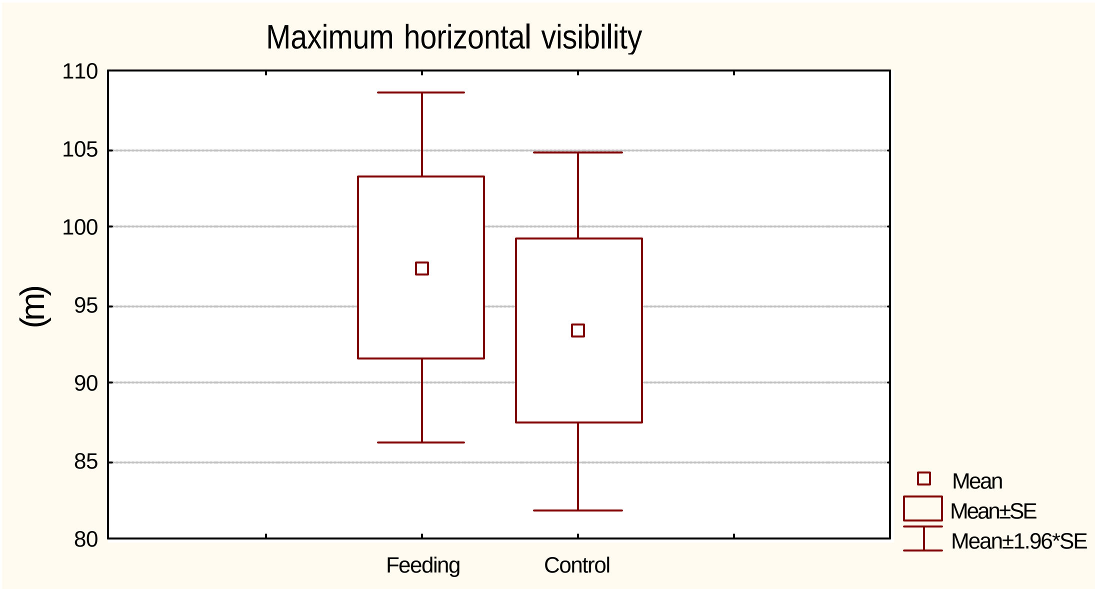


Sign test Z = 3.073399, p = 0.00

Figure 29: Box and Whisker Plot: Mean distance to drinking water. Feeding patches were significantly closer to water-holes than were control patches.

3.4.13 Maximum horizontal visibility

Feeding patches had a higher maximum visibility than did the control patches (Figure 30). Although this result was not significant, it none the less implies that their may be some woody structural or density threshold over which buffalo would avoid the site while feeding, as this may impede their ability to detect predators and/or maintain visual contact with the rest of the herd.

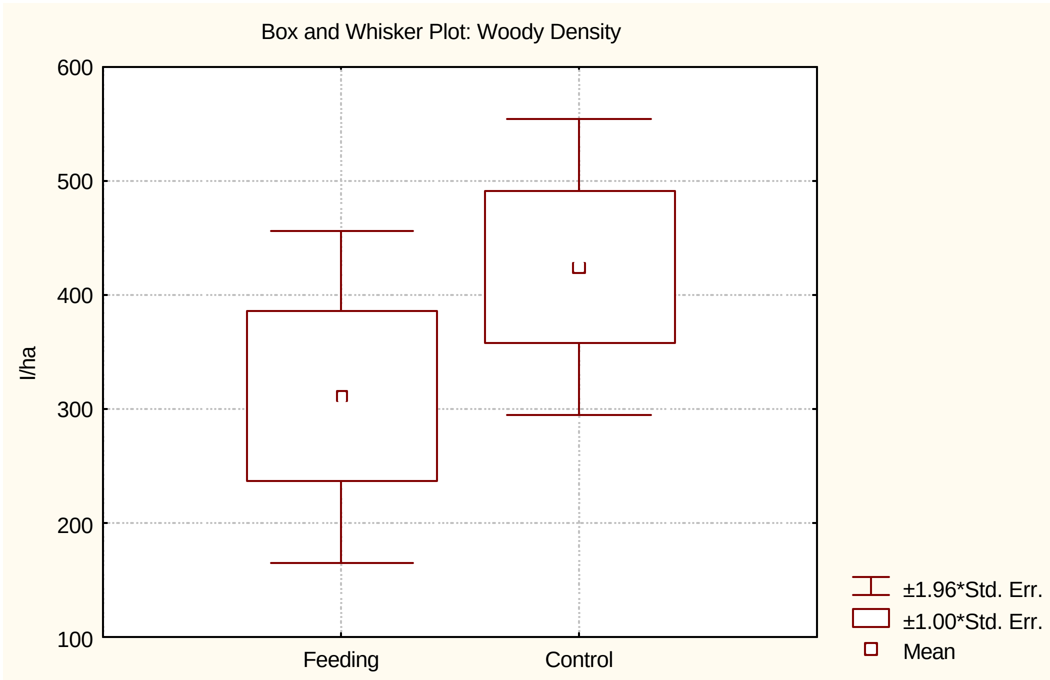


Sign test Z = 0.658586, p = 0.51

Figure 30: Box and Whisker Plot: Maximum horizontal visibility. Feeding patches computed a higher visibility index than did control patches.

3.4.14 Woody Density

Control patches computed a non-significantly higher woody density than feeding patches (Figure 31). This density estimate included all three growth forms namely, dwarf shrub, shrub and tree. The higher woody density in control patches led to an overall reduced maximum visibility for the herds.



Sign test Z = 1.401826, p = 0.17

Figure 31: Box and Whisker Plot: Woody density. Woody density was non-significantly lower in feeding patches than it was in control patches.

3.5 Results and discussion for variables not tested by pair-wise method

3.5.1 Mean grass height

A strong correlation between feeding and control patch grass height frequencies was computed across the six categories (Table 48). This indicates that grass height in feeding and control sites differed very little. In both the experimental and control patches ankle and knee height classes were most prolific. Buffalo thus seem to prefer grass tufts of a moderate height and avoid sites with especially tall tussocks. Control patches did have higher frequencies in extreme height class categories namely; very long grass tufts and bare ground, than did feeding patches. The results of the Spearman Rank Correlation test are presented in Table 49.

Table 48: Grass height class occurrence. The values listed in Table 48 reflect the number of grass tufts recorded in each of the height categories.

Height class category	Feeding	Control
Bare ground	153	243
Ankle	776	789
Knee	598	518
Waist	252	182
Shoulder	39	31
Grass >1500	2	20

Table 49: Results of Spearman Rank Correlation test. This table shows that grass heights were very similar between feeding and control patches.

	Valid N	Spearman R	t(N-2)	p-level
Feeding & Control	6	0.942857	5.659453	0.005

3.5.2 Geomorphological unit

A significant result was obtained (x_3^2 = 11.27, $p < 0.05$) for association of feeding patches with the valley bottom on annualised observations, and no seasonal division was included. Although the majority of these observations were made over the dry season, no significant result was obtained when observations were split into the two ecological seasons. No other catenal positions computed a significant association with buffalo use.

As buffalo are a water dependent species, drinking on average twice per day, selection of feeding patches in close proximity to water would limit unnecessary energy loss through walking; allowing buffalo to feed and rest near to available surface water. Figure 32 shows how a large number of feeding patches were located on the footslopes of the hillslope sequence, in close proximity to the surface water of the valley bottom. Figures 33 and 34 show the catenal distribution of patches in the dry and wet seasons respectively.

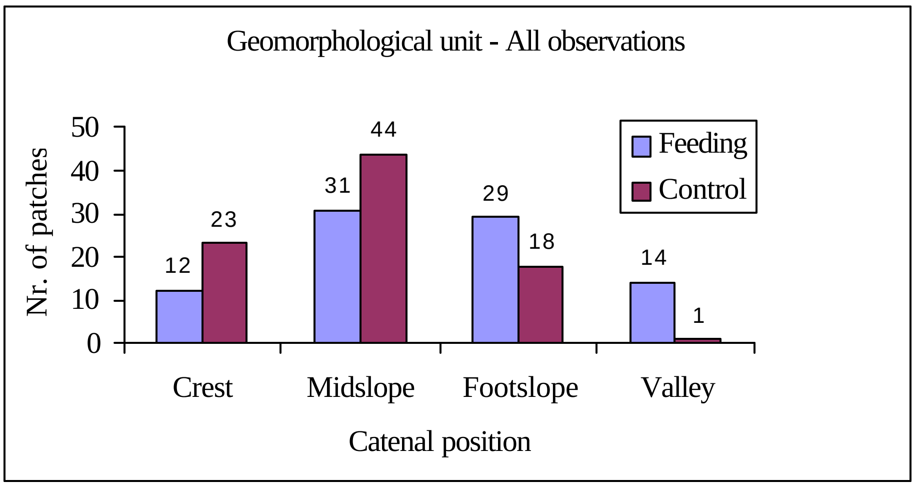


Figure 32: Geomorphological position of patches combined over both seasons. The lower portions of the hillslope sequence were preferred feeding patches.

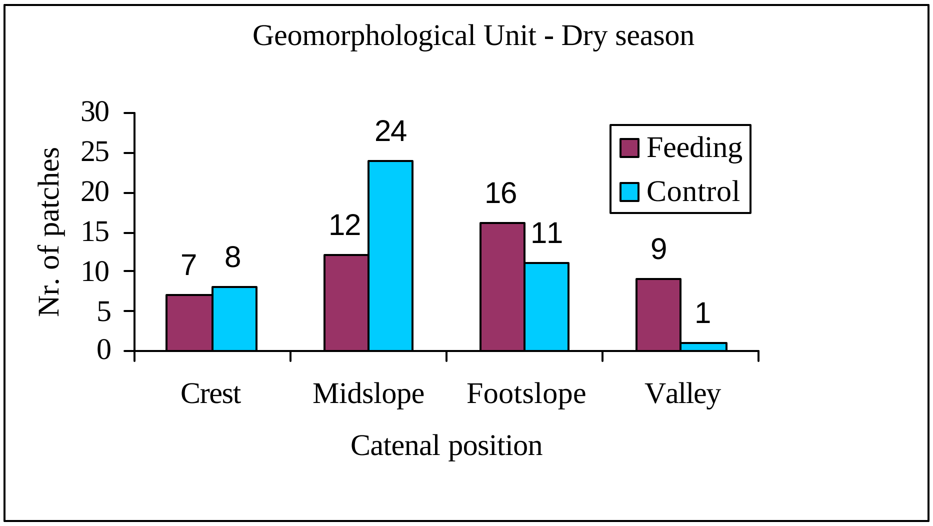


Figure 33: Geomorphological position of patches over the dry season. Over the dry season buffalo herds remained largely on the lower catena sequences.

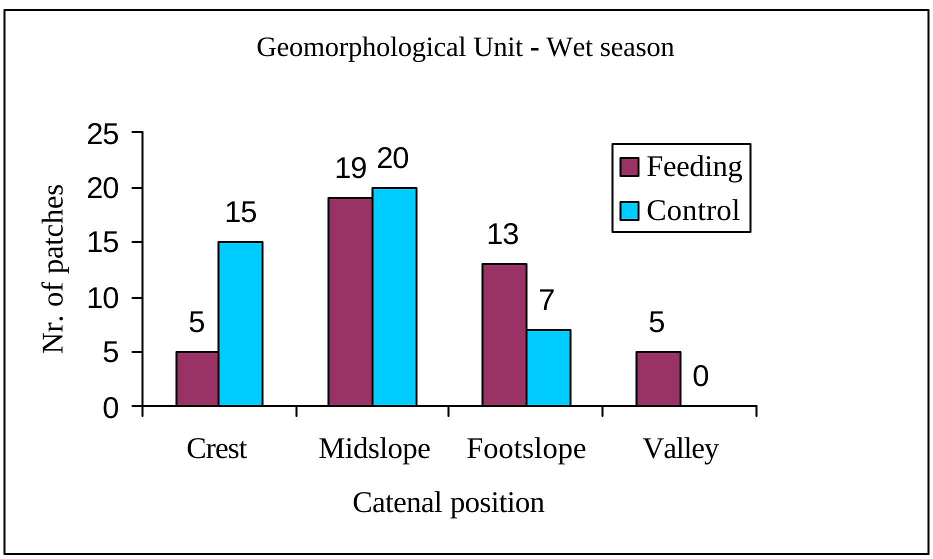


Figure 34: Geomorphological position of patches over the wet season. Buffalo herds used the range of catenas more evenly over the rainy season.

3.5.3 Aspect

None of the eight cardinal positions computed signif icant for association with feeding or control sites. However, by looking at Figures 35 and 36 it seems that the wet season feeding patches were well biased toward the southern and eastern aspects, while over the dry season a stronger bias was evident for north facing patches.

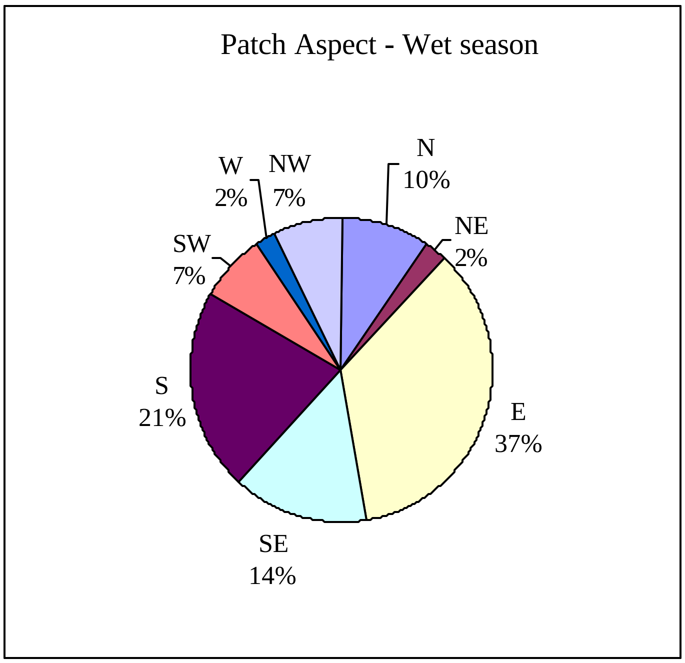


Figure 35: Aspect of feeding patches over the wet season (Summer). Buffalo herds showed a preference for East and South facing slopes over the hot summer months.

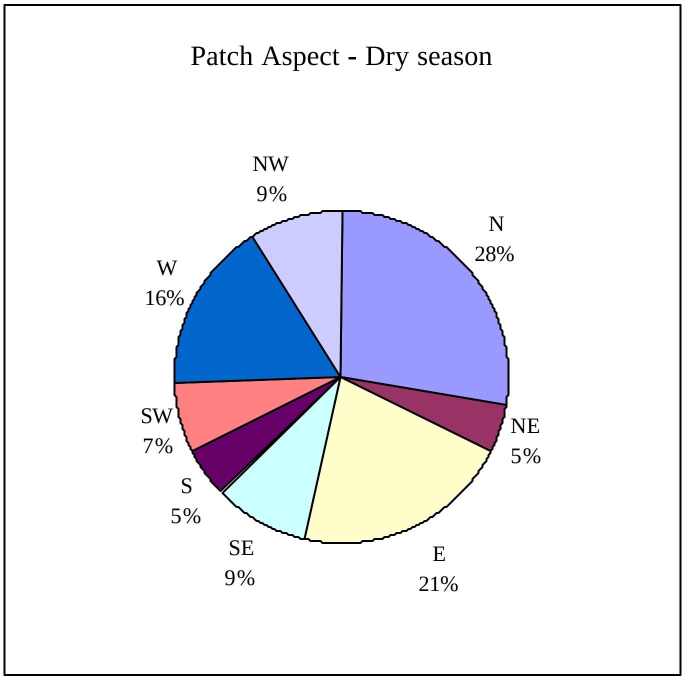


Figure 36: Aspect of feeding patches over the dry season (Winter). Buffalo herds showed a preference for the Northern slopes over the cooler winter months.

3.6 Summary and Conclusions

Absolute abundance of grass material, proved to be the most important variable determining buffalo selection of feeding patches over that of a neighbouring site.

Proximity of surface water was another important variable of feeding patch determination, as buffalo generally drink at least twice a day and often more frequently (Sinclair, 1977, Weir and Davidson, 1965) which would mediate the distance from which they can move in a day and within a range. This would also presumably be a factor when assessing coarser scale (Landscape level) habitat selection.

Buffalo showed a preference for the lower reaches of the catenal sequence, with the Valley Bottom computing significant, largely over the dry periods. The reasons would be two-fold. Firstly, patches that provide suitable forage and are close to surface drinking water would be highly sought after, as it obviates the need for herds to move great distances between these two key resources especially in the heat of the day, and over dry periods, when available energy reserves are lower and maintaining a more sedentary lifestyle would conserve vital body reserves.

Secondly, the attributes of the lower reaches of the hillslope, including higher soil moisture, often equates to greener, more palatable grass swards (Macandza *et al.*, 2004), containing higher nutrient content. This may be especially important over the dry season when a minimum crude protein content in the forage is necessary to maintain normal physiological processes; 7% was proposed for buffalo by Prins (1996)

Other patch dependent variables that were measured but did not compute statistically significant included, grass tuft moisture content, grass leaf percentage Nitrogen and Phosphorus and stem to leaf ratio, all of which were higher in feeding patches than were in control patches. Measuring of these variables may instead be more appropriate at the feeding station scale where buffalo decision-making involves choosing the grass tuft to feed on from what is immediately available to it. This selection will then be determined by the attributes of the grass tufts available, including grass greenness (inherently includes moisture content and percentage Nitrogen or crude protein and percentage Phosphorus) and stem to leaf ratios.

Maximum horizontal visibility was further in feeding patches although not significantly so. Prins (1996) claimed that it appeared that buffalo in Lake Manyara did not appear concerned with predation risk when choosing habitats. Preliminary data from studies conducted by Hay (In progress) shows that bulls that use habitats with poorer maximum visibility have a higher predation risk than mixed herds do that use relatively more open terrain. This would suggest that there may a critical woody density and conspecific maximum visibility, above which buffalo would generally avoid.

Herds chose patches that contained grass tufts of moderate height, showing a general avoidance for very tall tufts.

Seasonal variation in temperature was most likely responsible for the variation in aspect choice of feeding patches. Over the cold dry months the herds showed a bias toward the north facing slopes, optimising on the low angle of the sun during the winter solstice. The opposite was true in the wet months where most of the patches occurred on south and eastern slopes, presumably to avoid the heat of the day that's most intense through midday and early afternoon. Hence, southern and eastern slopes assist in achieving this aim.

Selection of one patch over a neighbouring one can be contributed to the overall biomass of available forage and the relative abundance of preferred grass species (as shown in chapter 1). The patch locale is mediated by distance to available surface water as well as the possible proximity of resting sites, the so-called "edge-effect" (Lamprey, 1963a).

4 Chapter 4: The influence of environmental variables on plant community structure and likely patch selection

4.1 Introduction

The analysis methods used thus far for this data set, phytosociological (chapter 1) and pair-wise (chapter 2), have used the presence or absence of plant species and other patch related variables respectively, to explore the differences in the patch characteristics of buffalo feeding and control sites. An analysis technique was required to combine all available data to explore the relationship between species presence/absence and abundance as well as patch dependent and independent characteristics. Canonical ordination allows one to relate the species composition of communities (patches) to their environment (variables) (ter Braak and Smilauer, 2002). The combination of exploratory and confirmatory techniques allowed me to explore the similarity/dissimilarity in community composition of feeding and control patches and confirm which unconstrained variables best explain community structure. Additional environmental variable permutations provided insight into the driving forces of feeding patch selection, corroborated statistically by the computation of critical probabilities. In effect this allows one to gain an insight into the determinants of patch selection tailoring in all available data in a single analysis technique. As stated by Quinn & Keough (2002), the aim is to reveal patterns in the data, especially among objects (patches) that could not be found by analysing each variable separately.

Ordination or scaling, allows one to plot these objects in multidimensional space, with the objects ordered along each axis, with the Euclidean distance between objects representing their biological dissimilarity (Quinn & Keough, 2002). The variation in the species data is explained via the ordination axes, which represent a theoretical explanatory variable (theoretical environmental variable or underlying gradient). A number of values are associated to each axis, one being the eigenvalue, which is an importance measure of that ordination axis. In matrix algebra an eigenvector $\underline{\tilde{o}}$ multiplied by a scalar value *ë* (lambda) satisfies the matrix equation of the square matrix $\underline{A}$.
Another is the gradient length, which represents a latent (theoretical) environmental variable, estimated in standard deviation (SD) units of species turnover. While species data are response variables (variables to be explained), environmental variables act as explanatory variables (predictors) to this data. Hence, species data are explained by the ordination axes and the environmental data are used to interpret or define these axes.

The aim of using ordination techniques for this analysis was to not only explain which environmental variables where responsible for community structure, as would be done in the classical sense, but rather to determine which variables (patch dependent and independent) were important drivers for buffalo patch selection.

4.2 Rationale for using CANOCO 4.5

A number of logarithmic errors were discovered in the previous version of CANOCO (version 3.12), which caused instability in the ordination axes, resulting in inconsistent results. The updated version 4.5 has corrected the errors and is thus a more accurate program to use. The discovered errors are mentioned below:

Tausch *et al.* (1995) observed that changing the order of species or samples in the input data file of the program DECORANA (Hill, 1979) can sometimes cause relatively large changes in the sample scores on the ordination axes. Oksanen & Minchin (1997) showed that CANOCO 3.12 suffered from the same type of ordination instability. They showed that the use of more stringent convergence criteria (in the power algorithm used to extract the ordination axes) gives results that are acceptably stable. In line with their proposals, CANOCO 4.5 uses a maximum number of iterations of 999 and a tolerance of 10^{-6}, which is between their strict and super strict tolerance criteria.
In DCA with detrending by segments, Oksanen & Minchin (1997) detected a bug in the subroutine SMOOTH that contributed to the instability, which has subsequently been corrected.

These improvements counter the scepticism expressed by Quinn & Keough (2002) to the use of DCA as an ordination technique, who questioned its arbitrary nature of detrending, its sensitivity to the number of segments chosen and problems with the order of data entry.

4.3 Materials and methods

4.3.1 Community (patch) structure

Ordination methods in CANOCO 4.5 (ter Braak & Smilauer, 2002) were used to describe the community structure of feeding and control patches and to see whether or not feeding and control patches would appear as discrete communities in the ordination diagram. While phytosociological methods were used similarly in the first chapter, abundance values of the species present in the patches were not taken in to account, only presence or absence. The ordination technique compares relative abundance of sites to create community structure. The relative abundance values for this data were the density estimates generated in Phytotab-PC for each species in each relevé. These data were for all growth forms that occurred within the patches; hence abundance data could be interpreted in structural terms too.

The final analysis excluded Relevé 71A as it contained only one graminoid species, namely *Lintonia nutans*, and consequently was an outlier from the rest of the relevés concerned in the analysis.

Indirect gradient analysis with a detrended unimodal response model was used in the form of Detrended Correspodence Analysis (DCA) for the ordination.

"Detrending-by-segments" was the detrending method used as recommended by Hill & Gauch (1980) for a DCA. It uses DECORANA's (Hill, 1979) default detrended correspondence analysis and obtains estimates of gradient lengths in standard deviation units of species turnover (SD). No transformation of the data was done, but downweighting of rare species was selected to avoid them having an unduly large influence on the analysis (ter Braak & Smilauer, 2002).

This technique was chosen for several reasons:

1. Hill & Gaugh (1980) amongst others, found faults with all other ordination techniques that are applied to ecological data specifying the occurrences of species in community samples.
2. Gauch *et al.* (1977) described the "arch effect" or "horseshoe effect" (Kendall, 1971) when using Canonical Analysis or Reciprocal Averaging, which is simply a mathematical artefact corresponding to no real structure in the data. This "arch effect" occurs when the gradient length of the first axes of the ordination diagram

exceeds four standard deviations (SD) (ter Braak & Smilauer, 2002), as was the case with these data. Linear response models (e.g. Principal Component Analysis (PCA)) are best suited when the gradients are short (<3 SD)).

3. Indirect gradient analysis gives an ordination that is calculated from the species data only, and hence shows major patterns in the species data irrespective of environmental data. Environmental data are then used to interpret the ordination diagram.
4. McCune (1997) showed that inclusion of noisy or irrelevant environmental variables can distort the representation of gradients in community structure, and use of indirect ordination methods show pure community structure without any constraint imposed by the environmental variables
5. Species data with many zeroes are often best analysed with a unimodal method (ter Braak & Smilauer, 2002), as was the case with this data set as not all species were present in all patches.

Stratification of the ordination diagram was used to determine the underlying environmental factors responsible for community structure, i.e. the unconstrained (those not only in the environmental variables file) environmental variables responsible for the separation of patches into communities sharing similar species assemblages. These unconstrained variables were the following:

- Geomorphological unit
- Aspect
- Substrate
- Season

4.3.2 Explanation of selection of patches explained by environmental data

Direct gradient analysis with a unimodal response model in the form of Canonical Correspondence Analysis (CCA) was conducted on the ordinated (detrended) data. Performing the ordination on just the community data via indirect means (DCA), and then using a CCA to relate the ordination to the environmental variables, allows an expression of pure community gradients, followed by an independent assessment of the importance of the environmental variables (McCune, 1997). This multivariate analysis was conducted on all the species data (selected patches and controls) to arrive at community groupings.

An ordination diagram with both samples and species can display either the relationships among samples or species in an optimal way, but not both; as the ordination axes of one are a linear rescaling of those of the other i.e. that the sample scores are weighted averages of the species scores. Hence, in the ordination diagram, species that occur in a sample lie around that sample's point. The variance of the sample score on each ordination axis reflects the importance of the axis as measured by the eigenvalue (the variance of the linear function of the variable in question), whereas the variances of the species scores along the axes are equal. The objective was to interpret relationships among samples from the ordination diagram, and hence, focussing the scaling on the "inter-sample distance" was chosen. Inter-sample scaling allows one to better infer environmental effect sizes.

Scaling type addresses the issue of how to infer the species data from the species-sample plot, other than by the centroid principle. Here Hill's scaling (Hill & Gauch, 1980) was chosen as it equalises the average niche breadth for all axes, and thus allows for long gradients and the distance rule.

Centroid principle – In a CA or CCA, a species score is a weighted average of the sample scores. Therefore, the species point in the ordination diagram is at the centroid of the sample points where it occurs. The samples that contain the species are thus scattered around that species' point in the diagram (ter Braak & Smilauer, 2002).

Distance rule – an extension of the centroid principle states that a sample that is close to the species point is more likely to contain the species than a sample that is far from the species point.

For a DCA the value for the scaling type may not be appropriate (ter Braak & Smilauer, 2002).

Irrespective of the scaling chosen the ordination diagram displays the major patterns in the species data table, the table of correlations between species and quantitative environmental variables (ter Braak & Smilauer, 2002).

4.3.3 Environmental variables included in CCA

The following environmental variables were used in the CCA, in order to determine their importance:

- Percentage (%) preferred grass species in relevé. A simple method was used to calculate a score for each relevé based on the percentage of preferred forage species present. Only the top five accepted grass species that remained important forage species throughout the year were used namely, *Panicum maximum* (63) *Panicum coloratum* (43), *Themeda triandra* (44), *Digitaria eriantha* (42) and *Urochloa mosambicensis* (40). The number in parentheses depicts the number of patches in which that species was utilised (accepted). This makes a total of 232 accepted "events" across all 5 species. The individual species acceptance value was then divided by 232 and multiplied by 100; to obtain a percentage of all accepted "events". For each relevé the total score of preferred species was calculated, with a maximum achievable score of 1 possible.
- Mean grass tuft density across all species in the relevé.
- Mean maximum visibility.
- Distance of the patch to water.
- Mean grass % Phosphorus of all species in the relevé.
- Mean grass % moisture of all species in the relevé.
- Mean grass % Nitrogen of all species in the relevé.
- Mean grass stem: leaf ratio of all species in the relevé.
- Grass: forb ratio.

4.3.4 Testing for statistical significance

The Monte Carlo permutation test was used to test the statistical significance of the relationship between the species and the whole set of environmental variables (ter Braak & Smilauer, 2002).

A permutation test calculates the probability of getting a value equal to or more extreme than an observed value of a test statistic under a specified null hypothesis by recalculating the test statistic after re-ordering (shuffling) of the data. This allows for the non-adherence to the strict assumptions associated with traditional statistical methods, which are generally not realistic in many practical situations (Anderson, 2001).

One of the strengths of the test is that the reference distribution is determined from the data themselves without the assumption of normality, homogeneity of variance and without mathematical derivations (ter Braak & Smilauer, 2002).

Forward selection of environmental variables was chosen in order to rank environmental variables in order of their importance.

Automatic forward selection was chosen using 9999 permutations (maximum) of the reduced-model Monte Carlo test. This results in the variables being selected sequentially on the basis of maximum extra fit (ter Braak & Smilauer, 2002). The reduced-model better maintains the Type 1 error probability in small data sets, and without covariables yields the exact Monte-Carlo significance level (ter Braak & Smilauer, 2002).

The unrestricted permutations option was chosen for permutation type under the randomisation model. Experimental and sampling design determines the appropriate permutation type. Unrestricted permutations are appropriate for completely randomised and randomised block designs and for simple random sampling and stratified random sampling. As buffalo selection of feeding sites was assumed random this option was deemed appropriate.

4.4 Results and discussion

4.4.1 Patch community structure

4.4.1.1 Feeding and control patches

All species and growth forms for both feeding and control patches were ordinated to determine if community structure differed between the two treatments.

No difference in community structure between the eighty-six feeding and eighty-six control patches is discernible from the Detrended Correspondence Analysis (DCA) ordination diagram (Figure 37), between the feeding and control patches. This shows feeding and neighbouring control patches overlap in terms of vegetation structure and species abundance. A strong unimodal response is seen with all four axes' gradient lengths exceeding four standard deviations (SD) (Table 50). Unimodal data implies that the species have their best performance around some environmental optima, as opposed to a linear response along an environmental gradient. Unimodal responses stress patterns in relative species abundance. Table 51 provides computations of a DCA on feeding patch data only; likewise Table 52 provides the results of a DCA on control patches only.

Table 50: Log table of results for DCA ordination of all **feeding and control** patches. The lengths of all the gradients are above 4 SD's, implying a strong unimodal response.

Axes	**1**	**2**	**3**	**4**	Total inertia
Eigenvalues	0.84	0.75	0.63	0.40	12.89
Lengths of gradient	4.40	5.54	4.47	4.06	
Cumulative percentage variance of species data:	6.6	12.4	17.2	20.3	

Table 51: Summary of log for **feeding** patch ordination by DCA. The first gradient shows a strong unimodal response, implying an explanatory variable exists for the choice of patch selected in feeding patches.

Axes	**1**	**2**	**3**	**4**	Total inertia
Eigenvalues	0.79	0.40	0.23	0.18	4.58
Lengths of gradient	4.97	3.04	2.62	2.69	
Cumulative percentage variance of species data:	17.3	26.1	31.1	35.0	

Table 52: Summary of log for **control** patch ordination by DCA. A strong unimodal response is computed for the first axis in control patches, implying a theoretical explanatory variable exists that explains avoidance of control patches.

Axes	**1**	**2**	**3**	**4**	Total inertia
Eigenvalues	0.62	0.42	0.2	0.18	4.85
Lengths of gradient	4.99	3.92	2.36	2.72	
Cumulative percentage variance of species data:	12.8	21.5	25.7	29.5	

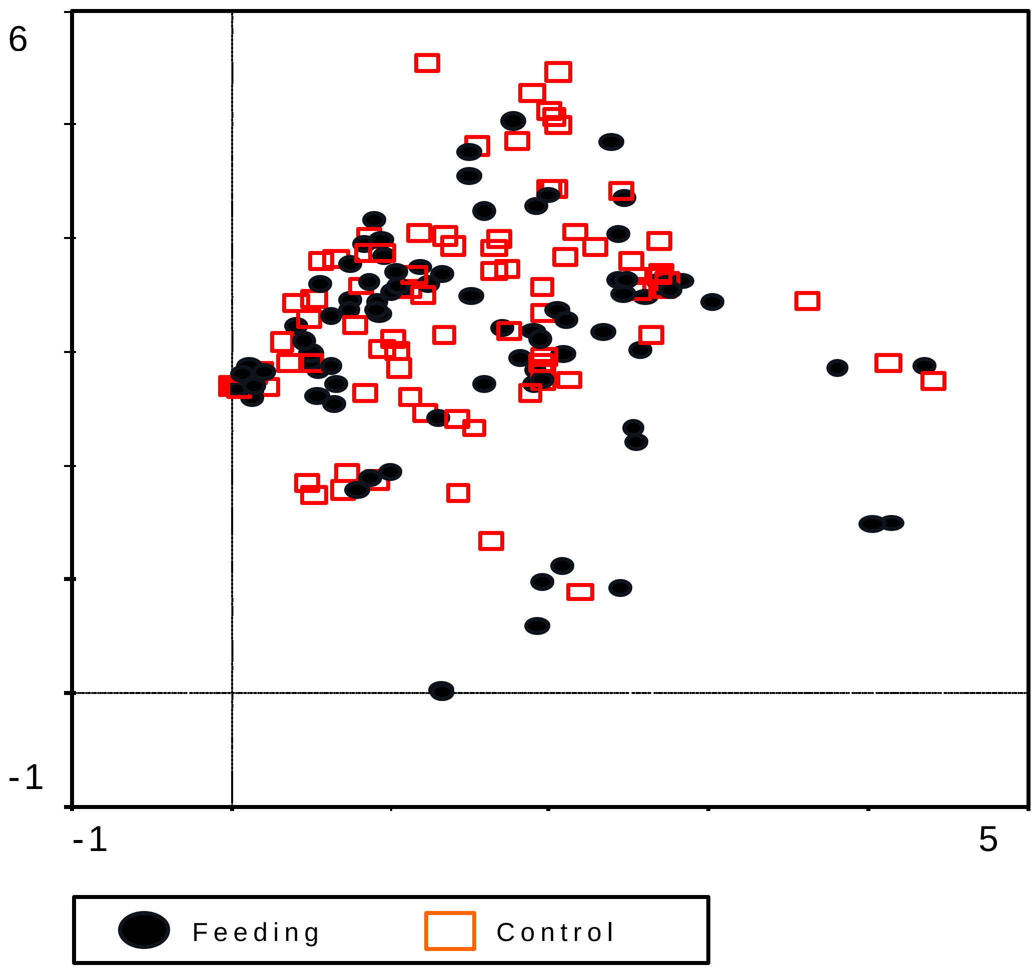


Figure 37: Ordination diagram showing the position of feeding and control patches in ordination space, with both feeding and control patches evenly distributed in the diagram.

4.4.2 Patch herbaceous structure

4.4.2.1 Feeding and control patches

To ensure that the presence of multiple growth forms wasn't obscuring a possible pattern in the herbaceous layer, all growth forms, apart from the grasses, were excluded from the ordination. Many of the forbs appear seasonally or only in certain years when suitable conditions prevail, possibly unduly affecting classification.

The ordination diagram (Figure 38) shows that there is also very little difference in the herbaceous community structure between the two treatments.

Ordination of feeding and control sites by DCA showed a strong unimodal response with the first axis exceeding four standard deviation units (Table 53).

Table 53: Log of DCA for both **feeding and control** sites, using only grass species and not all growth forms. Similarly, with the ordination of all growth forms (Table 50) a strong unimodal response is computed for the first axis.

Axes	**1**	**2**	**3**	**4**	Total inertia
Eigenvalues	0.77	0.39	0.22	0.18	4.913
Lengths of gradient	4.10	3.33	2.89	2.60	
Cumulative percentage variance of species data:	15.6	23.5	28.0	31.7	

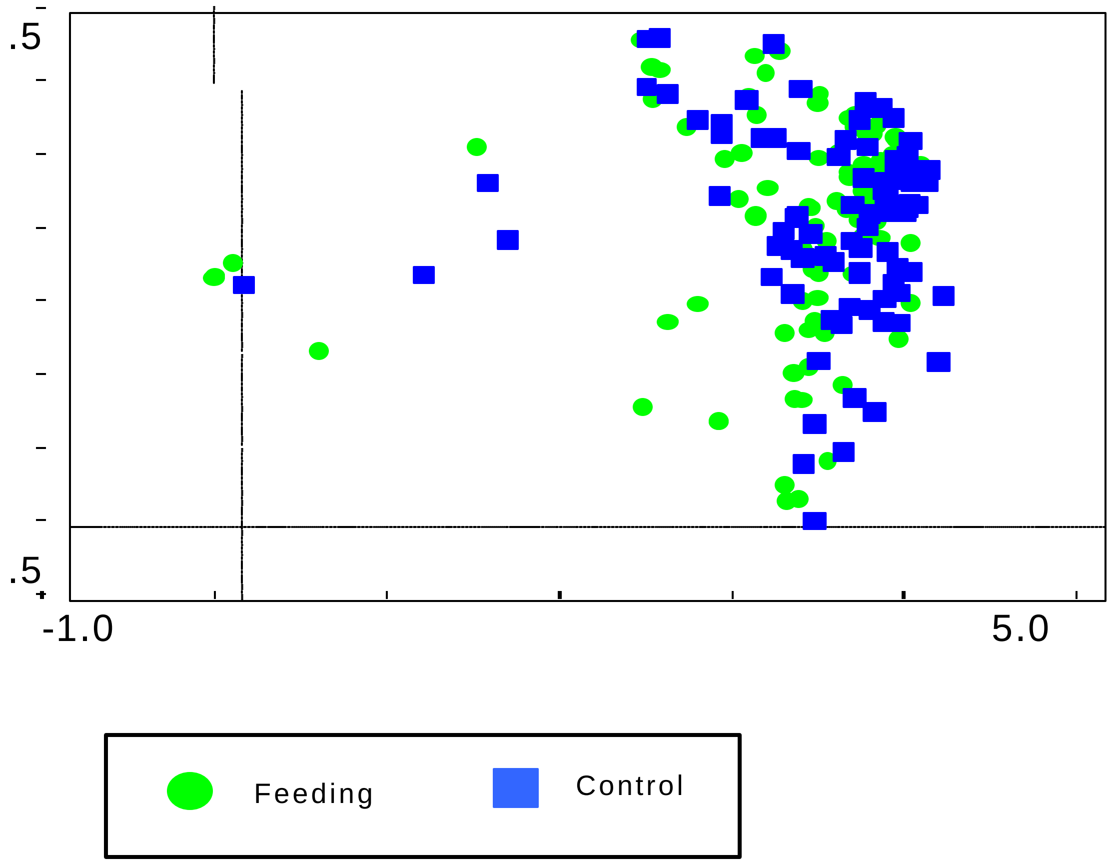


Figure 38: Simple ordination diagram showing the position of feeding and control sites when only the grass species are included in the ordination, and all other species and growth forms are excluded. Feeding and control patches occur marginally on opposite sides of the diagram.

4.4.2.2 Basalt and Granite relationships

The strongest ordination relationship was found to be with underlying substrate, showing that community structure and the observed ordination of patches, was instead related to soil type and geology. Figure 39 shows the distribution of grass species only, but the same pattern also exists when all species and growth forms are used. This pattern is largely due to the fact that the two focal herds studied occurred on different substrates, namely basalt and granite/gabbro. This shows the difference in community structure and floristics associated with the two focal herds. While the difference in community structure between granite and basalt patches is shown in ordination space, as occurring on separate sides of the ordination diagram, the Euclidean distance between them is not large, implying that buffalo foraging criteria share many similarities, irrespective of the substrate.

Hence, buffalo in the study region source patches that have an abundance of similar preferred grass species, irrespective of the substrate that dominates their home range. The ordination diagram was also used to explore other factors that might explain the distribution of the patches in ordination space, including geomorphological unit, season and aspect. No pattern was found for these variables.

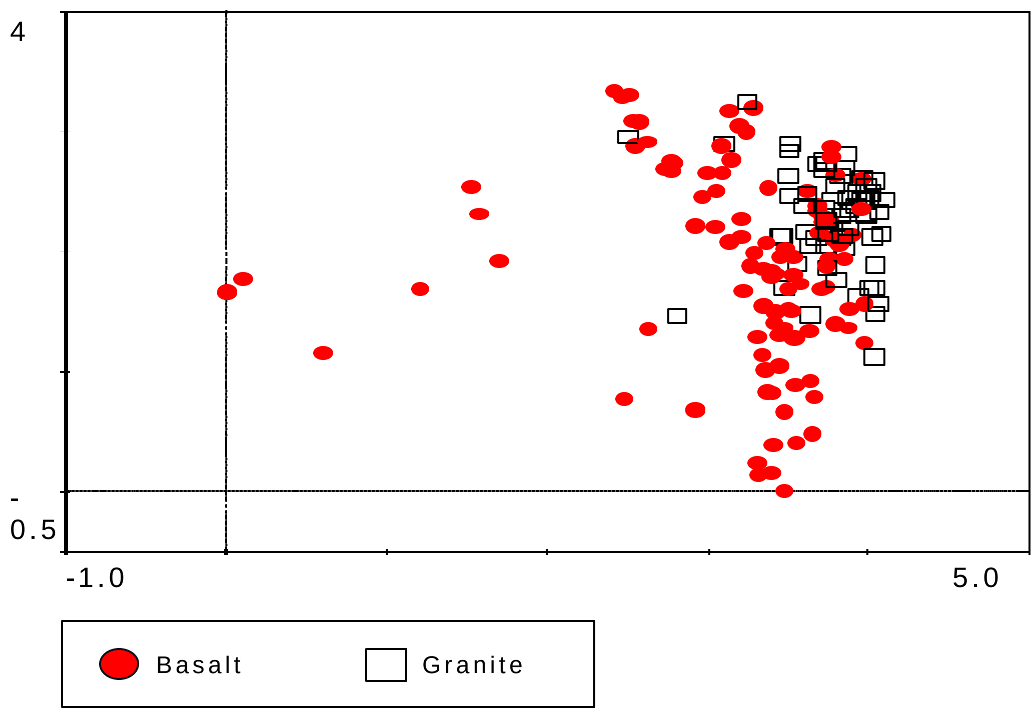


Figure 39: Simple ordination diagram showing distribution of basalt and granite sites, only including the grass species and not all other species and growth forms. Basalt and granite patches show a small amount of separation in the ordination diagram, implying a degree of similarity in species composition and abundance.

4.4.2.3 Underlying substrate effects and herd foraging strategies

Figure 40 shares many similarities to Figure 39, except that the graph shows the distribution of the two focal herds feeding patches, inclusive of all species and growth forms and not only the herbaceous species. Herd M's home range was exclusively on the basalt's, seen as black dots on the right hand side of the diagram, while herd T's home range was largely restricted to the granites, red squares mostly confined to the left hand side of the diagram, but included portions of basalt during the early wet season. The diagram also shows that both herds feeding patches show a degree of overlap due to similarities in patch floristics.

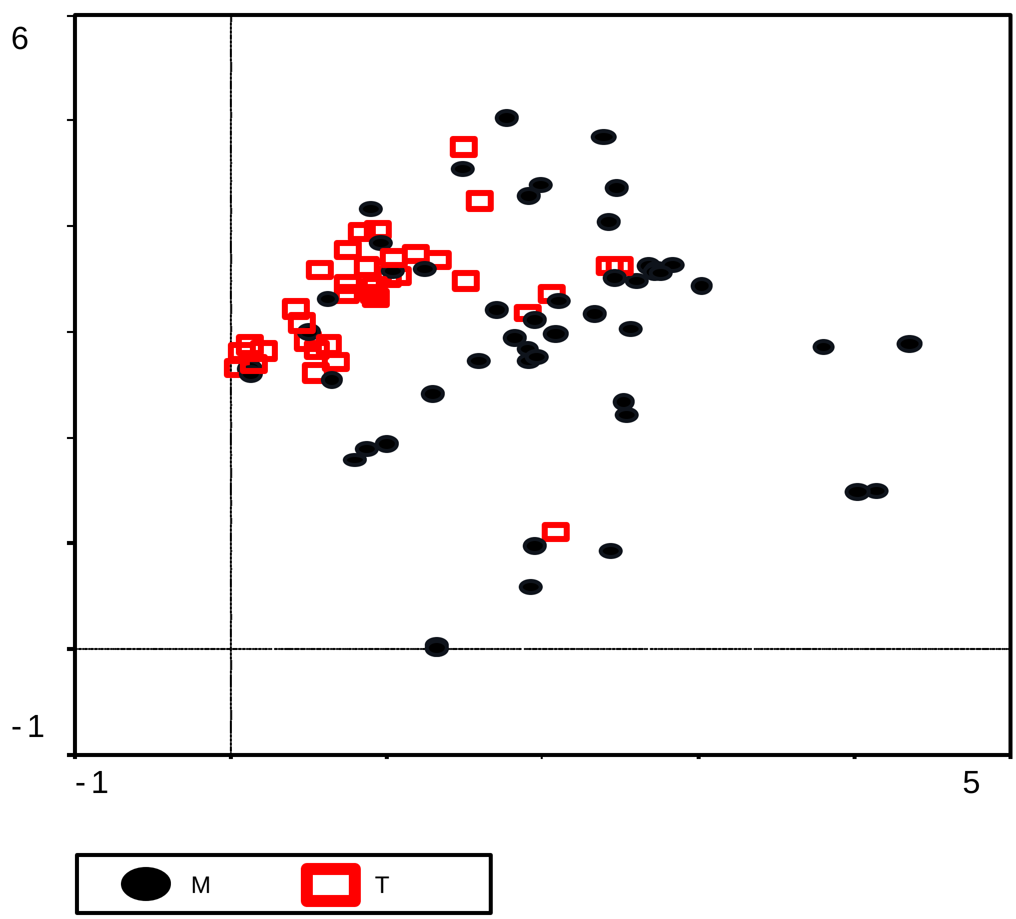


Figure 40: Position of feeding patches of both study groups in ordination space. The diagram strongly resembles Figure 39 as the two herds portrayed occurred on opposite ends of the study area on fundamentally different substrates.

4.4.2.4 Species occurrence in feeding patches

According to the "Centroid principle" and its extension, the "Distance rule", the proximity of species to the sample sites in an ordination diagram shows the significance of the species to the floristic composition of the sites. Figure 41 highlights the dominant species in buffalo feeding patches. To assist with clear inspection of the diagram some of the species had to be marginally shifted allowing the names to be easily read. This was only necessary where dense clustering of labels occurred in the diagram. The labels were not moved to another area of the diagram, as this would lead to inaccurate interpretation of the data, but instead remained in the appropriate area of the diagram. The apparent inability of buffalo to select for nutritious plant parts is circumnavigated by selecting patches containing a high proportion of preferred foodstuffs, obviating the need for highly selective foraging behaviour. The species occurring in the centre of the sampling points were *Panicum maximum*, *Panicum coloratum*, *Digitaria eriantha*, *Themeda triandra*, and *Urochloa mosambicensis*. The centroid principle ensures that the species that are present and dominant in the majority of the patches occur toward the centre of the diagram. This however, is not always the case as the distance rule can on occasion counteract the centroid principle in so much as it ensures that a species is represented closest to the patch or patches in which they occur. The problem occurs when the species are in fact an isolated occurrence and the patch in which it occurred is by chance centrally positioned in the ordination diagram, thus placing the species centrally too. *Fingerhurthia africana* and *Eragrostis cilianensis* are examples in point, where they occurred in two and three patches respectively, and by chance the patches to which they are affiliated are in the centre of the diagram. The full species names for the abbreviations occurring in the diagrams can be found in Appendix 10.

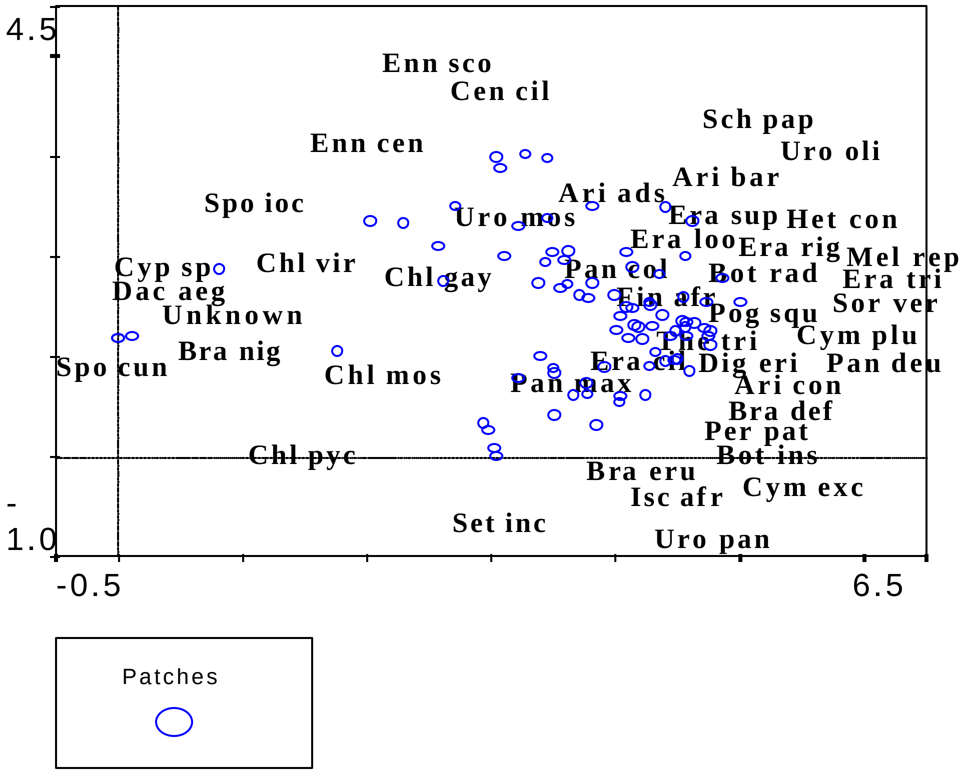


Figure 41: Grass species position in ordination space. The position of species, determined by the centroid principle, means that the species occurring at the centre of the diagram are those found most abundantly in the majority of feeding patches.

4.4.2.5 Grass species contribution in patches on basalt substrate

The majority of the feeding patches are relatively closely clustered in ordination space, accounting for the high unimodal response of the ordination. Governed by the centroid principle the grass species' occurring closest to a cluster reflect their dominance in those patches. These species are largely those identified as preferred forage species (Macandza *et al*., 2004) that also dominated the patch in terms of their abundance. The balance of the species appearing on the perimeter of the diagram, are the species occurring at very low frequencies. The species proving most important on patches occurring on basalt substrate were *P. coloratum, U. mosambicensis, C. ciliaris* and *P. maximum.* A weak moisture gradient is visible in the diagram (Figure 42) with the species occurring on the more arid patches positioned on the right hand side, progressing to more mesic patches on the left hand side of the diagram.

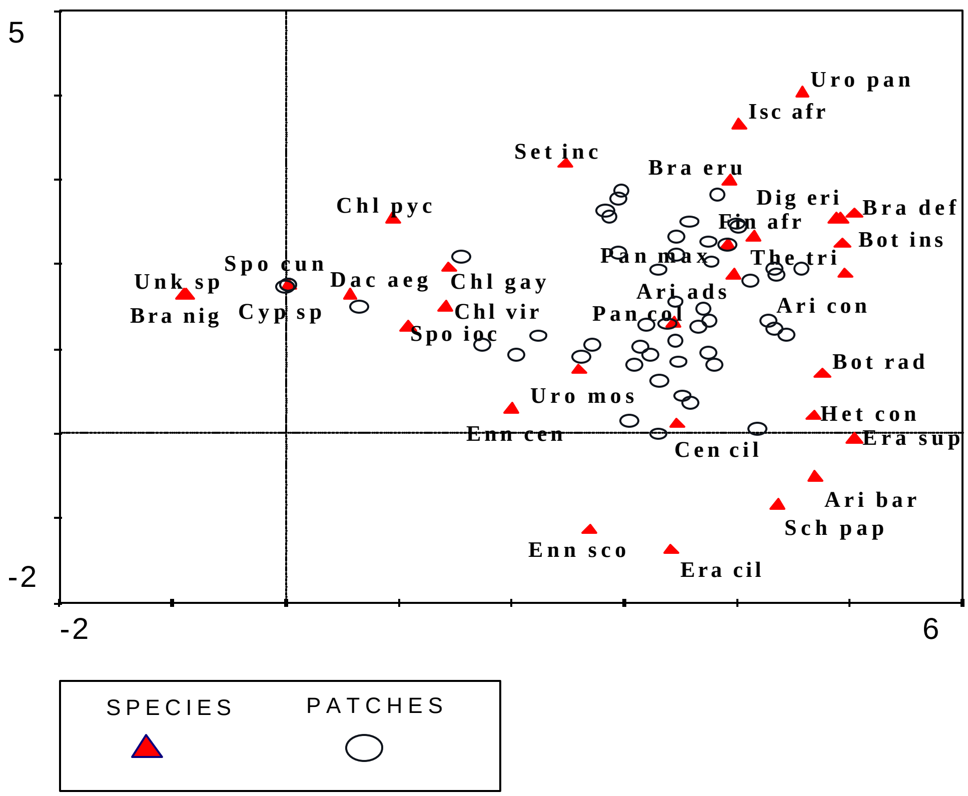


Figure 42: Ordination diagram reflecting the species contributing most significantly to the floristic composition of the sample sites occurring on basalt substrate

4.4.2.6 Grass species contribution in patches on granite substrate

D. eriantha, U. mosambicensis, T. triandra and *Eragrotis superba* dominated the core region of the sample sites for the granite/gabbro soils; while *P. coloratum* and *P. maximum* occurred more on the periphery of the sample sites cluster (Figure 43). As previously mentioned these diagrams do not always accurately reflect the dominant species that occur in the majority of the patches in the core of the sample cluster. Certain species that only occur in a single patch may be situated in the centre of the diagram not due to the centroid principle but rather due to the distance rule, with the patch that the species occurs in, coincidentally located in the centre of the diagram. This is the case for unknown species (*Unk* sp.) that were only recorded in two patches, yet occurs in the centre of the patch cluster.

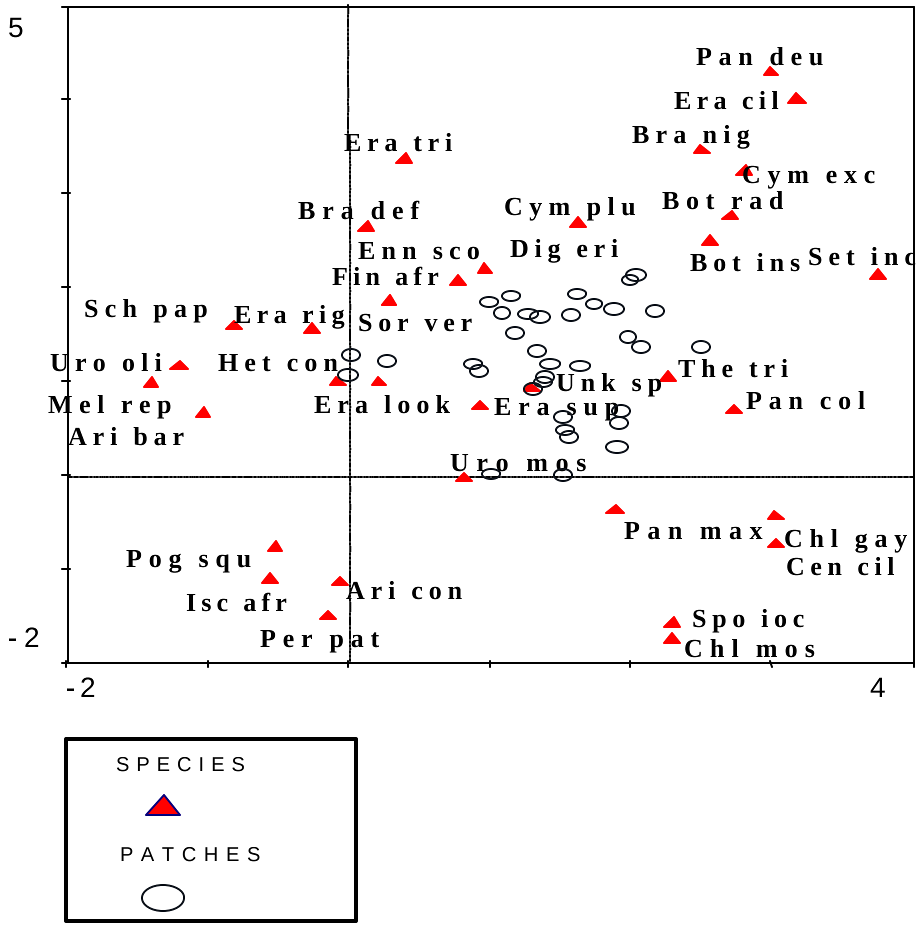


Figure 43: Ordination diagram of feeding patches on granitic/gabbro soils showing the relative importance of different grass species to their floristic composition (as governed by the centroid principle and distance rule).

4.4.2.7 Species occurrence in control patches

The control patches had mostly unpalatable species dominating the core area of the sample sites in figure 44; including *Botriochloa insculpta, Botriochloa radicans, Dactyloctenium aegyptium, Eragrostis cilianensis, Brachiaria deflexa, Aristida congesta* subsp. *barbicollis* and *Eragrostis trichophora.* The fact that control sites were largely dominated by less palatable species, is a clear driving force for buffalo herds to select one patch over a neighbouring one. This suggests that buffalo may have the cognitive ability to differentiate between species of grass and make quantitative evaluations between available foraging sites as to where the optimum ratios of preferred forage exists.

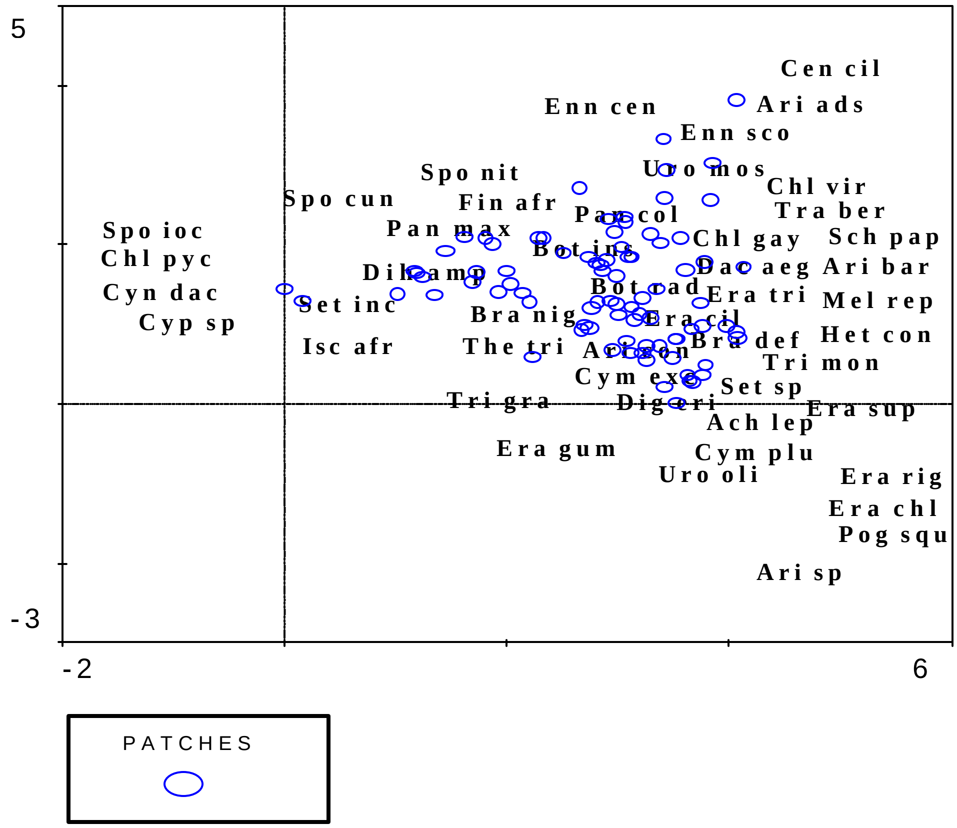


Figure 44: Diagram showing the dominant species in control patches. The grass species largely avoided by buffalo in this study are centrally located in the diagram; meaning they were dominant species in control patches.

4.4.2.8 Selection of feeding patches explained by environmental data

Species abundances might explain one of the reasons why buffalo select between neighbouring foraging patches, but the inclusion of patch dependent and independent variables may assist in explaining additional reasons. As previously highlighted the proportion of preferred species within the patch determined whether or not that patch was utilised. This comes out in the canonical correspondence analysis of environmental variables (Figure 45) as being the primary driver for selecting the patch. The second factor was the relative abundance of grass tufts, expressed as tuft density. Hence, there needs to be a high biomass of preferred species relative to a neighbouring site. Maximum visibility was the third factor determining patch selection implying that easy predator detection may be an important consideration for buffalo while foraging, as relatively few animals are vigilant at this time. It may also be coincidental that open sites contain a higher percentage of preferred grass species. Distance to drinking water was another significantly important variable.

The balance of the variables related primarily to the grass' chemical and physical attributes, with percentage Phosphorus computing significant. This result was unexpected as the permutation results are generally consistent with those of the pair-wise analysis.

It is recognised that in this analysis there was a combination of scale effects that may be complicating the analysis, and that grass chemical and physical attributes are not necessarily unimportant foraging variables; but may not be instrumental at this scale on deciding on which patch to select, but may be important at a finer scale when the individual animal chooses which grass to bite.

The results computed by the CCA are found in Tables 54 and 55 below:

Table 54: Marginal effects of CCA. Percentage preferred grass species in feeding patches explained the most variability in the analysis.

	Marginal Effects	
Variable	Var.N	Lambda1
% Pref sp	9	0.27
Tuft density	5	0.23
Mean visibility	1	0.16
Dist to water	2	0.13
Grass %P	7	0.12
Grass Stem: leaf	8	0.11
Grass %N	6	0.1
Grass %Moisture	4	0.07
Grass:Forb	10	0.06

Woody density	3	0.04

Marginal effects - list the individual environmental variables in order of the variance they explain singly, i.e. when that environmental variable is used as the only environmental variable (lambda-1 column).

Table 55: Conditional effects of CCA. Percentage preferred species, tuft density, mean visibility, distance to water and percentage leaf phosphorus all computed significant contributors to patch selection.

Conditional Effects				
Variable	Var.N	LambdaA	P	F
% Pref sp	9	0.27	0.000	5.2
Tuft density	5	0.19	0.001	3.95
Mean visibility	1	0.11	0.011	2.14
Dist to water	2	0.09	0.033	1.93
Grass %P	7	0.09	0.017	1.95
Grass %Moisture	4	0.06	0.201	1.26
Grass %N	6	0.06	0.328	1.11
Grass stem: leaf	8	0.03	0.701	0.8
Grass: Forb	10	0.04	0.674	0.76
Woody density	3	0.02	0.949	0.41

Conditional effects - shows the environmental variables in order of their inclusion in the model, together with the additional variance each variable explains at the time it was included (lambda-A) and, if Monte-Carlo tests were asked for, the significance of the variable at that time (P-value) together with its test statistic (F-value). A variable contributes significantly (at the 5% significance level) to the model of already included variables if the P-value is less than or equal to 0.05.

Figure 45: CCA diagram illustrating relative importance of environmental variables in feeding patch selection. The length of the vector depicts its importance. The more important the vector is to the patch or set of patches, the closer it will be to them. The vectors and a brief explanation of each used in Figure 45 is given below:

1. Tuft density - a grass abundance index; referring to how closely packed the grass tufts are.
2. Mean visibility – the mean measurement of the four maximum measurements taken at 1.5m in each patch.
3. % moisture – the mean percentage moisture content of the grass species for the patch.
4. % P – mean percentage Phosphorus of each patch.
5. S:L – mean stem to leaf ratio of the grass tufts in each patch.
6. %N – mean percentage leaf Nitrogen of the grass tufts in each patch.
7. G:F – grass to forb ratio of each patch.
8. Dist to Water – the distance of each patch from the nearest water source.
9. Woody density – the combined density of all woody growth forms for each patch.

10. % Pref sp. – the relative percentage of preferred species occurring in each patch.

4.4.2.9 Importance of environmental variables in control patches

None of the variables tested computed significant under the Monte Carlo permutation test (Tables 56 and 57). Distance to water, grass: forb ratio, mean visibility and stem: leaf proportion were the important effects (Figure 46), both marginally and conditionally.

Table 56: Marginal effects of CCA. Distance to water and grass to forb ratio explained the most variability in control patches.

	Marginal Effects	
Variable	Var.N	Lambda1
Dist to water	2	0.15
G:F	10	0.15
Mean visibility	1	0.1
S:L	8	0.09
Tuft density	5	0.07
%N	6	0.06
% pref sp	9	0.05
%P	7	0.05
Woody density	3	0.03
%Moisture	4	0.03

Table 57: Conditional effects of CCA. Distance to water and grass to forb ratio explained the most variability in control patches; as it did in the marginal effects analysis (Table 56). None of the tested environmental variables computed significant for control patches.

	Conditional Effects			
Variable	Var.N	LambdaA	P	F
Dist to water	2	0.15	0.118	1.47
G:F	10	0.15	0.106	1.54
Mean visibility	1	0.1	0.412	0.99
S:L	8	0.1	0.492	0.96
%N	6	0.1	0.373	1.07
% pref sp	9	0.07	0.799	0.66
%Moisture	4	0.06	0.855	0.63
%P	7	0.08	0.752	0.72
Tuft density	5	0.05	0.897	0.52
Woody density	3	0.05	0.981	0.41

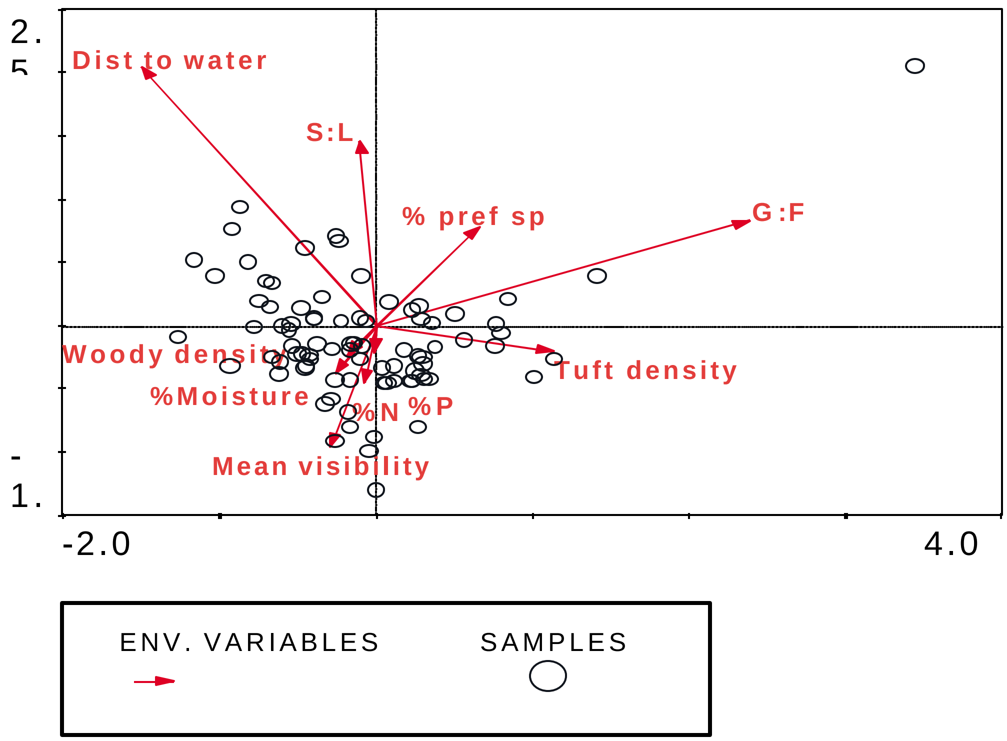


Figure 46: CCA of control plots, showing relative importance of environmental variables.

The vectors and a brief explanation of each used in Figure 46 is given below:

1. Tuft density - a grass abundance index; referring to how closely packed the grass tufts are.
2. Mean visibility – the mean measurement of the four maximum measurements taken at 1.5m in each patch.
3. % moisture – the mean percentage moisture content of the grass species for the patch.
4. % P – mean percentage Phosphorus of each patch.
5. S:L – mean stem to leaf ratio of the grass tufts in each patch.
6. %N – mean percentage leaf Nitrogen of the grass tufts in each patch.
7. G:F – grass to forb ratio of each patch.
8. Dist to Water – the distance of each patch from the nearest water source.
9. Woody density – the combined density of all woody growth forms for each patch.
10. % Pref sp – the relative percentage of preferred species occurring in each patch.

4.5 Summary and Conclusions

Ordination of the feeding and control patches did not separate the two treatments in ordination space but instead they shared a large overlap. This alludes to fact that the community structure of the two treatments does not differ significantly. Both the feeding and control patches showed a strong unimodal response, providing evidence that some environmental optima were coupled to the patches. One might expect this to be the case with feeding patches, as the high species selectivity exhibited by the herds must be coupled to certain environmental factors.

Ordination effectively allows one to search for patterns and relationships in the data. This pattern was based on the underlying substrate, whereby a fairly clear division was observable between granite and basalt patches. No similar pattern was found with geomorphological unit (catenal position), season or aspect.

Interpretation of the species data in the ordination diagram revealed that feeding patches were comprised of a higher abundance of preferred forage species than were control patches. Governed by the centroid principle, *P. maximum*, *P. coloratum, D. eriantha, T. triandra,* and *U. mosambicensis* were positioned centrally in the feeding patch diagram, meaning that the species point in the ordination diagram is at the centroid of the sample points in which it occurs. Conversely, control patches contained mostly unpalatable, avoided species in the central portion of the diagram, implying that the reason herds avoided these patches was due to an inadequate proportion of preferred grass species. The avoided species included *B. insculpta, B. radicans, D. aegyptium, E. cilianensis, B. deflexa, A. congesta* and *E. trichophora.*

Feeding patches on the basalt plains consisted predominantly of *P. maximum, P. coloratum, C. ciliaris, U, mosambicensis*, and *T. triandra*, while patches on the granites were comprised mostly of *D. eriantha, T. triandra, E. superba* and *U. mosambicensis*. This shows while occurrence of certain species may vary due to geological constraints, there was a high degree of overlap in species composition of feeding patches across both substrate types.

Canonical Correspondence Analysis (CCA) of patch dependent and independent variables revealed that the percentage of preferred species in a patch explained the most variability in the data. Tuft density, maximum visibility and the distance to the nearest drinking water were then the most important variables determining patch selection.

5 Chapter 5: Forage selection of herds

5.1 Introduction

Fundamental to the understanding of all scale-related herbivore habitat selection is the knowledge of what the primary forage requirements of an animal are in terms of plant species composition and the species dependent factors that might determine these food preferences. Food selection at the plant species level has been well documented for buffalo (Sinclair, 1977; Prins, 1996; Macandza *et al*., 2004; Pienaar, 1969; de Graaf *et al.*, 1973; Stark, 1986; Vesey-Fitzgerald, 1974; Leuthold, 1972; Perrin & Brereton-Stiles, 1999; Hansen *et al.*, 1985) and the relationship with nutritive values and plant structure of the plant species concerned (Sinclair & Gwynne, 1972; Field, 1976; Mugangu *et al*., 1995). Two of the above-mentioned publications on feeding selection were conducted in the KNP, namely Pienaar (1969) and Macandza *et al.* (2004). Pienaar (1969) collected 100 rumen content samples during routine culling operations in the Crocodile Bridge region of the park (south eastern region). The full microscopic analysis was never completed and only a limited number of stomach contents were analysed, yielding a preliminary record of species eaten. Interestingly, he listed the following five species that appeared to be preferred throughout the year, *Themeda triandra, Panicum coloratum, Digitaria* sp*., Panicum maximum* and *Heteropogon contortus*. Macandza *et al.* (2004) found *Panicum maximum, Panicum coloratum, Cenchrus ciliaris* and *Heteropogon contortus* to be important forage species over the late dry season for buffalo herds in the central Satara region. These results compare closely with my findings, implying that buffalo forage selection shows consistent trends both spatially and temporally in the KNP. In fact, while species distributions will vary across geographic expanses, inspection of species lists cited by other authors (Wentzel *et al*., 1991; Macandza *et al*., 2004; De Wet, 1988; Pienaar, 1969) show that a number of grass genera are commonly selected and rank consistently among the preferred species of buffalo.

A number of studies have shown that not only are buffalo capable of selecting for plant species, but also for plant part. Sinclair & Gwynne (1972) examined the rumen contents of buffalo in the Serengeti at different times of the year, to determine if the behavioural selection of grass species appeared to be concerned with maximising the nutrient quality of the food requirements. They showed that buffalo exhibited a preference for species with a high leaf to stem ratio, commonly accepted as a caveat for nutrient quality as leaves contain higher crude protein than do stems (Owen-Smith, 1982). Field (1976) analysed the more important grasses to buffalo, chemically and physically. Stem to leaf ratio is considered to have influenced the species eaten, as was the percentage green leaf of selected grasses. A negative response to the silica presence in dead leaves was also observed. These factors act as a combination of attractants and repellents that determine how the animal responds (Field, 1976). His observations suggest that selective grazing enables a herbivore to consume a diet of significantly higher nutritive value than that of the average sward.

The rationale for my work was not intended to give detailed quantitative data on buffalo forage selection, but rather highlight broad trends throughout the year that would help place patch selection criteria into perspective. If animal decision-making is indeed hierarchical in nature, decisions made at a lower level in the hierarchy e.g. feeding station, will directly influence and contextualise those made at a higher level.

5.2 Materials and methods

Within each 20x10m quadrat, used to determine the characteristics of the feeding patch, a subjective estimate of species utilisation was conducted. This aimed to track species preferences through the year and to note to what degree they were utilised. The degree of utilisation was related to two aspects, namely

1. The percentage of the available tufts of that species that were utilised within the quadrat and,
2. The proportion of the individual tufts of that species that was removed by bites.

The utilised tufts were classified into one of the three following subjective categories: high (majority of a species' tufts were removed), moderate (some utilisation of a species' tufts removed, but not extensively) or light (very little utilisation).

This estimation was conducted by extensively walking throughout the quadrat and recording all species that had been utilised by the herd, thus producing a seasonal species preference inventory, relating to its abundance (density) within the site, and it's seasonal nutritive values.

Figures 47 and 48, showing changes in species selection through the year, were generated using data collected by Macandza *et al*. (2004) during the late dry season of 2002. I then continued to collect the same data following the same methodology to complete a calendar year worth of longitudinal data of the changes in species selection.

5.2.1 Statistical analysis

Pearson's product moment correlation coefficient (Statsoft, 2004) was used to test if a linear relationship existed between grass species acceptance and a number of grass tuft attributes, including phytomass, percentage leaf Nitrogen and Phosphorus and Stem proportion. This was done in order to gain an insight into why certain grass species are preferred over others.

Multiple Linear Analysis (Statsoft, 2004) was also used to test for interactive effects on grass acceptance between independent variables. The general purpose of multiple regression analyses is to identify any relationship between several independent or predictor variables and a dependent or criterion variable (Statsoft, 2004).

5.3 Results and discussion

5.3.1 Grass species preferences

A detailed report of the species that occurred in feeding patches over both the wet and dry season and their categories of degree of utilisation are listed in Appendix 2. Appendix 3 lists, in order of preference, the species that occurred in feeding patches and indices of selection. Table 58 provides an overview of the number of patches the species occurred in and the degree of utilisation of the five most preferred species, for both seasons.

Table 58: Summary of the five most preferred grass species. Utilisation class specifies the modal category in which most observations were made for that species.

Species	Season	No of patches	Utilisation class (mode)
Panicum maximum	Wet	30	Heavy
	Dry	33	Heavy
Themeda triandra	Wet	18	Moderate
	Dry	26	Moderate
Panicum coloratum	Wet	20	Moderate
	Dry	23	Light
Digitaria eriantha	Wet	19	Heavy
	Dry	23	Heavy
Urochloa mosambicensis	Wet	18	Light
	Dry	22	Light

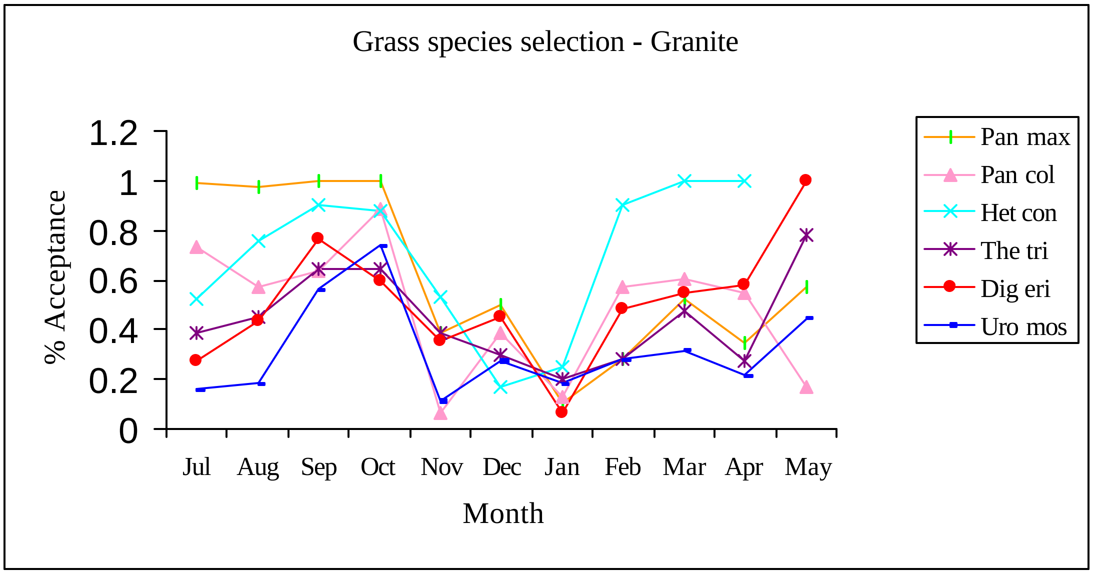


Figure 47: Grass species acceptance of herds on granitic soils throughout the year. Figure 47 shows how selectivity for the more commonly utilised grasses varies over the year (expanded from Macandza *et al.*, 2004). The abbreviated values in the legend refer to the following species: Pan max – *Panicum maximum*, Pan col – *Panicum coloratum*, Het con – *Heteropogon contortus*, The tri – *Themeda triandra*, Dig eri – *Digitaria eriantha*, Uro mos – *Urochloa mosambicensis.*

Highest levels of acceptance of preferred species are seen over the dry months when grass species selection peaks. The corollary to this may occur at the very end of the dry season when availability of these species is scarce, and buffalo may need to supplement their diets with previously avoided species (Macandza *et al.*, 2004). The drop in acceptance of all species over the wet months equates to an increase in the variety of species accepted. Due to wetter conditions more species are likely to be palatable over this period. The variation in acceptance is demonstrated in Figure 48.

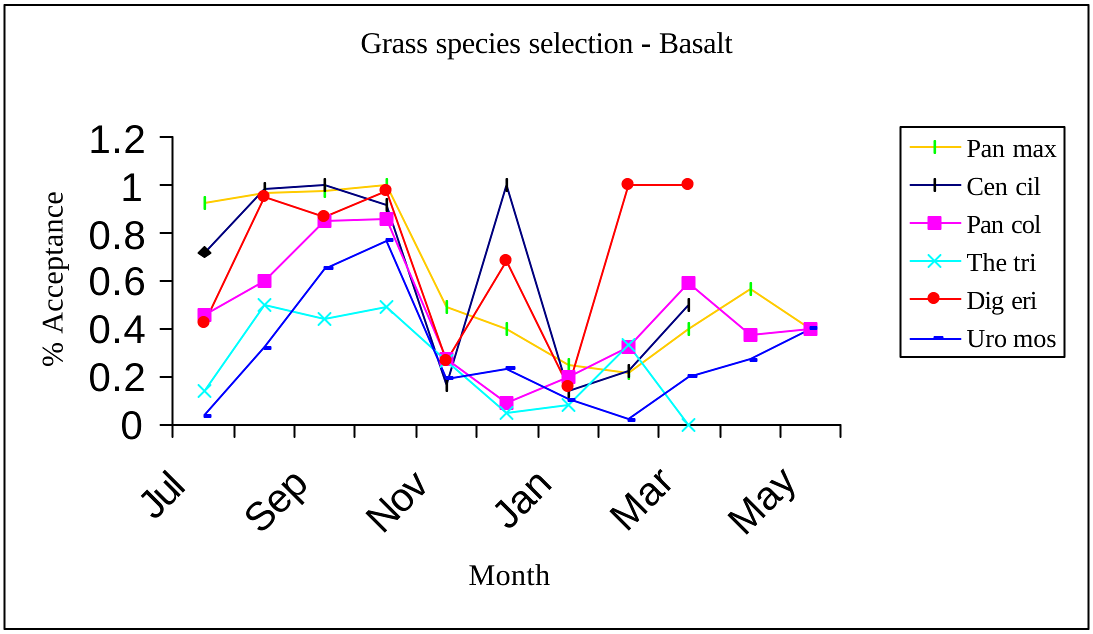


Figure 48: Grass species acceptance throughout the year by herds on basalt soils. The study period spanned 16 months resulting in some months including data for both years (2002 and 2003) (expanded from Macandza *et al*., 2004). The abbreviated values in the legend refer to the following species: Pan max – *Panicum maximum,* Cen cil – *Cenchrus ciliaris,* Pan col – *Panicum coloratum,* The tri – *Themeda triandra*, Dig eri – *Digitaria eriantha*, Uro mos – *Urochloa mosambicensis.*

A similar pattern to the granites is apparent on the basalt with exception of *C. ciliaris* and *D. eriantha*, which were highly accepted over the wet season. This was due to late rains and the subsequent need for buffalo to utilise especially *C. Ciliaris*, which retains its greenness well into the late dry season along the riverine reaches. The small amount of rainfall that fell in November may have improved soil moisture conditions on the granitic soils, but would only have an ephemeral impact on soil moisture on the basalt soils due to their higher CEC (cation exchange capacity). This would necessitate the herds to revert to the riverine areas until more substantial rainfall arrived in February.

5.3.2 Physical and chemical influences on species acceptance

Grass physical and chemical properties are highly variable for a given species even within a localised area. An example may be a tuft of *Panicum maximum* that occurs on the southern side of a tree compared with a conspecific on the northern side. Due to increased exposure to direct sunlight, particularly over the winter months, and a subsequent increase in evapotranspiration, it is likely that the tuft on the northern side will have lower moisture content. This was clearly evident while working in the field, whereby a grass tuft below a tree or shrub would be greener on its southern side than on its northern side. Hence, trying to investigate the relationship between acceptance and average values for grass species' attributes within a patch is fraught with difficulty. Using the average value for the attribute in question may not accurately reflect the choices the animal makes. An animal within a localised area might select for a specific forage attribute from a given species that it may only find in certain of the available tufts.

5.3.2.1 Phytomass

The relationship between grass acceptance and phytomass showed the strongest relationship (r=0.36) (Figure 49). Acceptance is defined as the number of feeding patches in which that grass species was utilised, irrespective of the degree of utilisation. As buffalo are commonly accepted as bulk-grazers, with the need to fill a capacious rumen, this result comes as no surprise. The fact that the relationship is relatively weak suggests that several grass attributes combined may be needed to determine selection criteria.

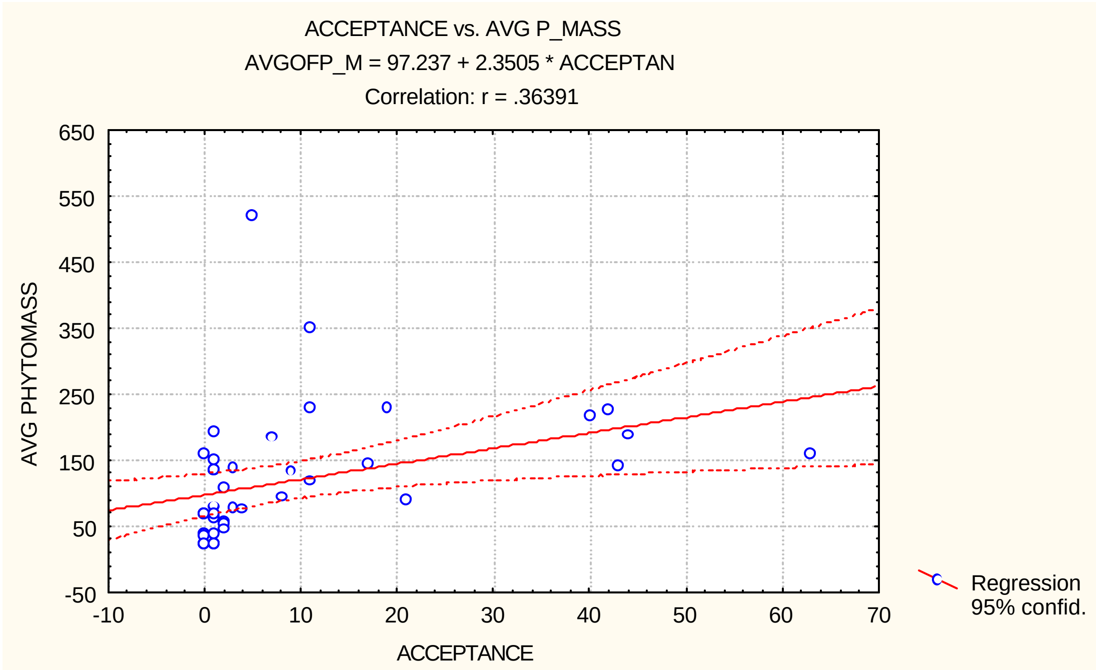


Figure 49: Grass acceptance as a function of phytomass. The number of patches in which a grass is eaten is plotted against the species' phytomass (kg/ha). The linear relationship between phytomass and "Acceptance" (r=0.36) is not strong.

5.3.2.2 Percentage leaf Nitrogen content

No correlation was found between mean acceptance and mean percentage leaf Nitrogen content (Figure 50). This however, does not imply that crude protein content of the grass is not an important selection criterion. The leaf Nitrogen content measurements are only mean values for the patch, and not actual measurements from the specific tuft selected. Animals select at multiple scales, and the methodology used in this study was intended to measure larger patch scale variables, and may not have been appropriate to ascertain fine-scale differences in forage selection. Foraging information was collected in order to contextualise the larger-scale patch selection and place selection criteria in perspective.

Other studies have indeed shown crude protein to be a deciding factor in forage selection (Mugangu *et al.*, 1995; Field, 1976; O'Reagain & Mentis, 1989).

A relatively strong positive linear relationship exists between tuft moisture content and percentage leaf Nitrogen content (r=0.59) (Figure 51). This relationship would presumably be stronger had the leaf moisture content (not the entire tuft, which includes the stems) been compared with the percentage leaf Nitrogen content. Figure 44 shows that no correlation exists between grass acceptance for a given species and its percentage leaf Nitrogen content.

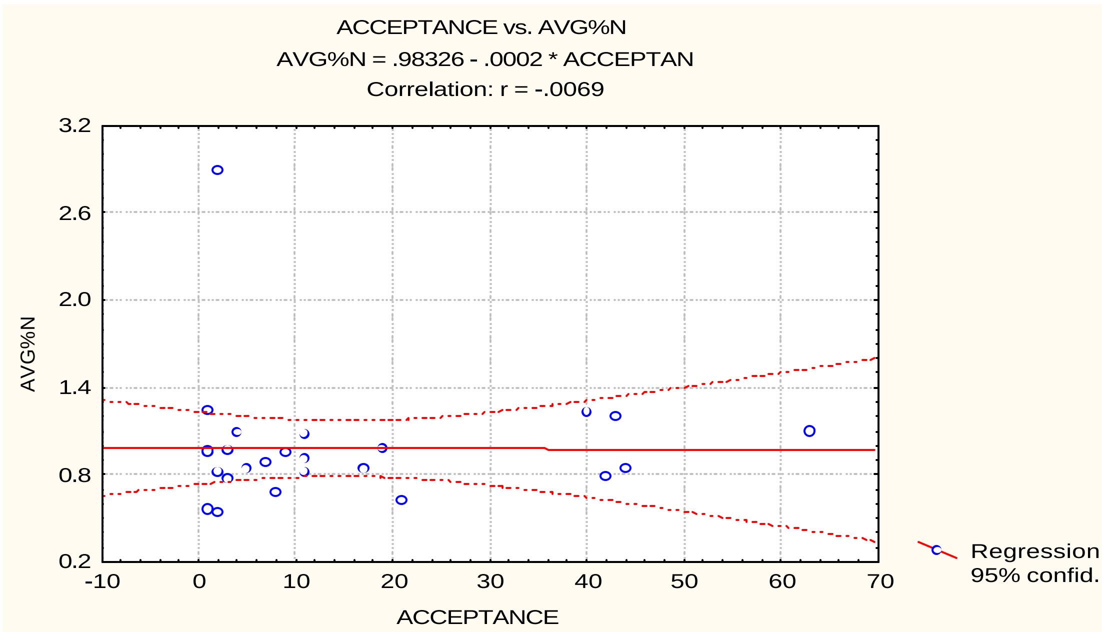


Figure 50: Grass acceptance and its correlation with percentage leaf Nitrogen content. There is no relationship (r=0.0069) between "Acceptance" and percentage grass leaf Nitrogen content.

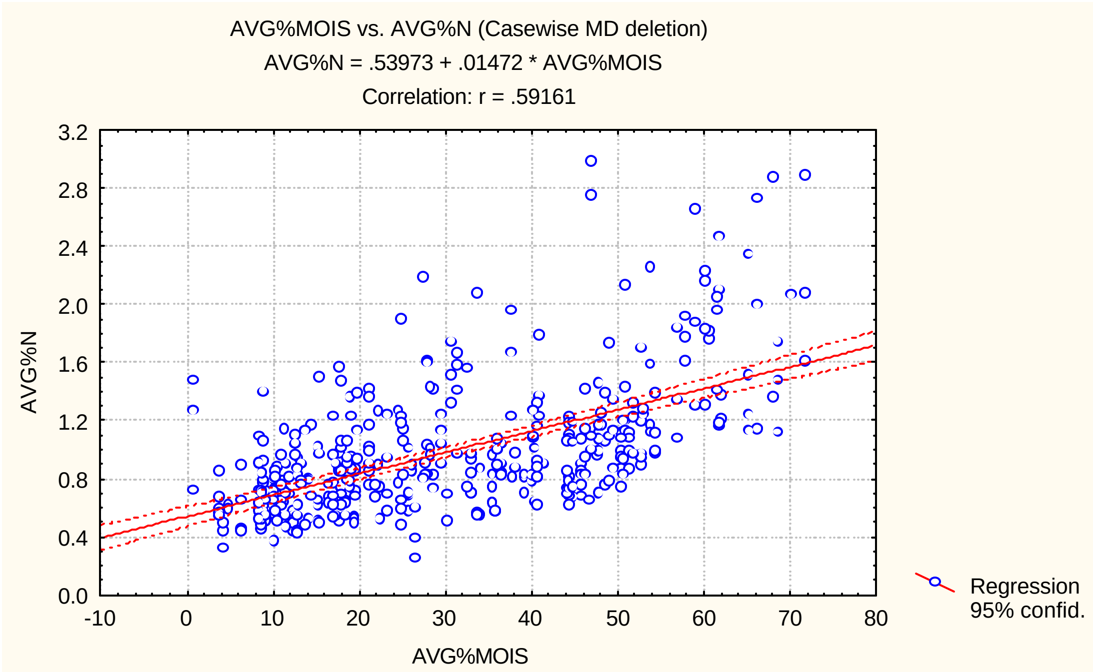


Figure 51: Linear relationship between mean percent grass moisture content and mean percentage leaf Nitrogen content. A moderately strong relationship (r=0.59) is computed.

5.3.2.3 Percentage leaf Phosphorus content

A non-significant correlation was computed between mean acceptance and mean percentage leaf Phosphorus content (Figure 52). Wallis de Vries & Schippers (1994) found Phosphorus content of forage proved relatively significant in determining habitat occupancy of free-ranging cattle. Once again, the sampling design employed may not have been suitable to detect fine-scale differences in grass leaf Phosphorus content. It may also be possible that different nutrient and mineral components may be important at different times of the year and even to different age groups of animals, when that nutrient is in limited supply or when animal physiological demands for it are highest (e.g. during foetal development). Analysing such data across seasons and amalgamated age groups may hide such finer relationships. Wallis de Vries & Schippers (1994) stated the following: "The importance of minerals as a potential factor in the differentiation of habitat use advocates the consideration of a variety of nutrients in foraging models. Habitat selection then becomes a decision process during which time is allocated to different habitats in proportion to their supply in several required nutrients".

Most optimal foraging models use energy or protein as the important variable to be maximised (Wallis de Vries & Schippers, 1994). However, many studies have suggested a selection of complimentary nutrients (Rapport, 1980; Thomson *et al.*, 1987; Belovsky, 1990) rather than looking solely for linear relationships with a single nutrient or mineral. Grass moisture content also determines the quantity of Phosphorus contained in the leaves (Figure 53). The relationship is weak, but still shows the influence of grass moisture content on leaf phosphorus content.

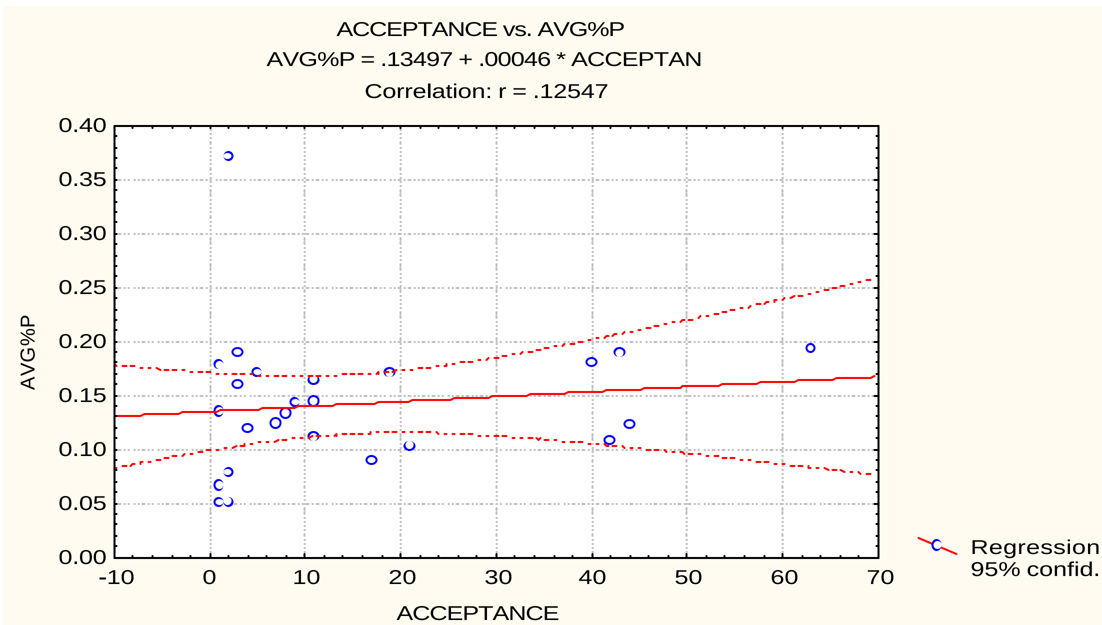


Figure 52: Grass acceptance correlated to percentage leaf phosphorus. A very weak relationship (r=0.12) was computed between percentage Phosphorus and "Acceptance".

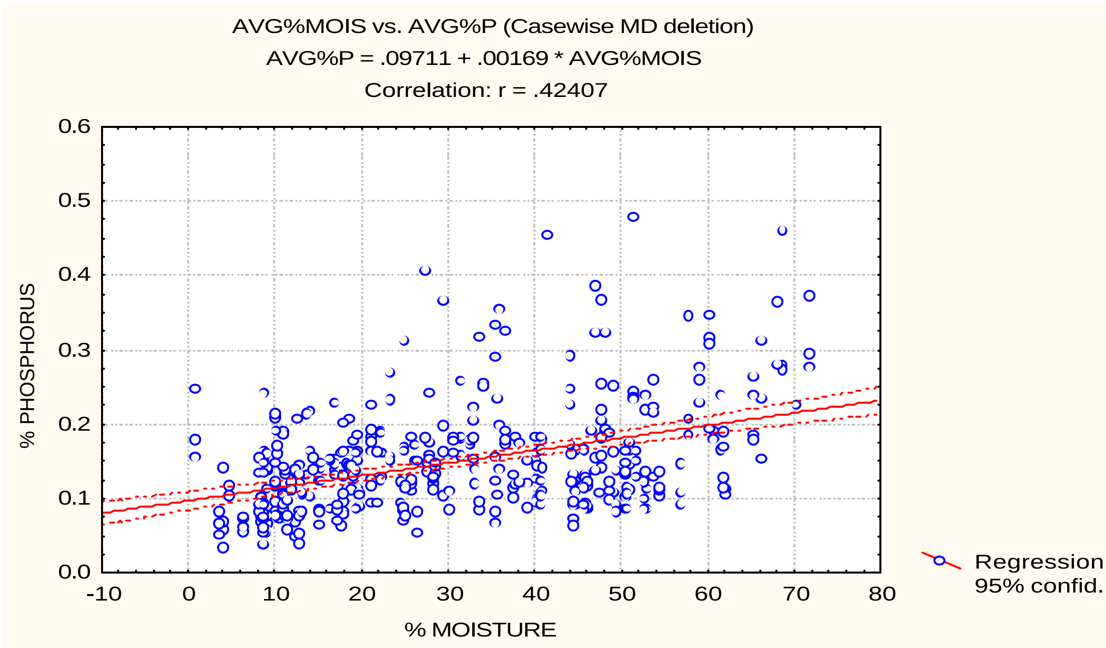


Figure 53: Linear relationship between percentage leaf Phosphorus content and percentage plant moisture content. A moderately strong relationship (r=0.42) was computed between leaf Phosphorus and grass moisture content; less so than between leaf Nitrogen and grass moisture content though (Figure 51).

5.3.2.4 Grass stem to leaf ratio

No relationship between grass stem to leaf ratio and species acceptance was evident (Figure 54). Several other studies have found the stem to leaf ratio to be an important selection criterion in forage selection (Sinclair & Gwynne, 1972; O'Reagain & Mentis, 1989; Mugangu, 1995). The high frequency of acceptance of *D. eriantha* by herds on the granitic soils may be due in part to its low stem proportion.

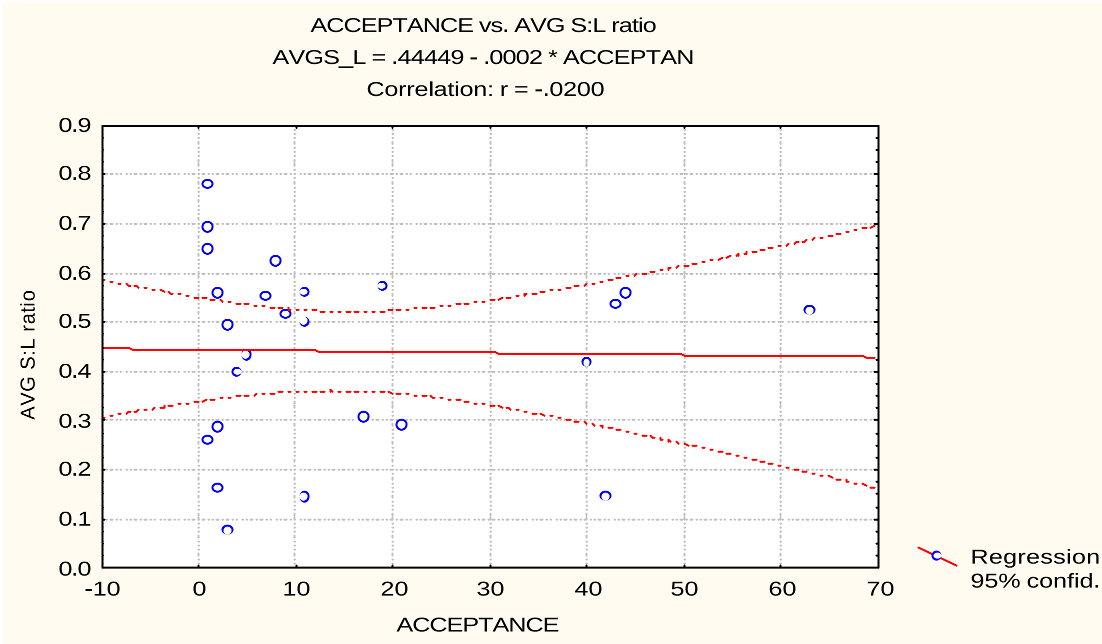


Figure 54: The linear relationship of grass acceptance with grass stem to leaf ratio. A mild inverse relationship (r=-0.02) exists between grass stem proportion and "Acceptance".

5.3.2.5 Percentage grass moisture content

Surprisingly, a negative correlation between acceptance and percentage grass moisture content was computed (r=-0.18) (Figure 55). Moisture content is likely to be the most variable attribute both temporally and spatially. A tuft of grass below a thicket of shrubs will retain a higher moisture content than one transpirating in a clearing in the midday sun. A tuft may even lose moisture within a 24 hr period if soil moisture is low and transpiration rates are high. Hence, not sampling the specific tufts utilised combined with time delays between time visited by the herd and sampling, may all prove problematic in trying to deduct real differences.

Field (1976) found a positive relationship between buffalo preference and the proportion of green leaves of the selected species.

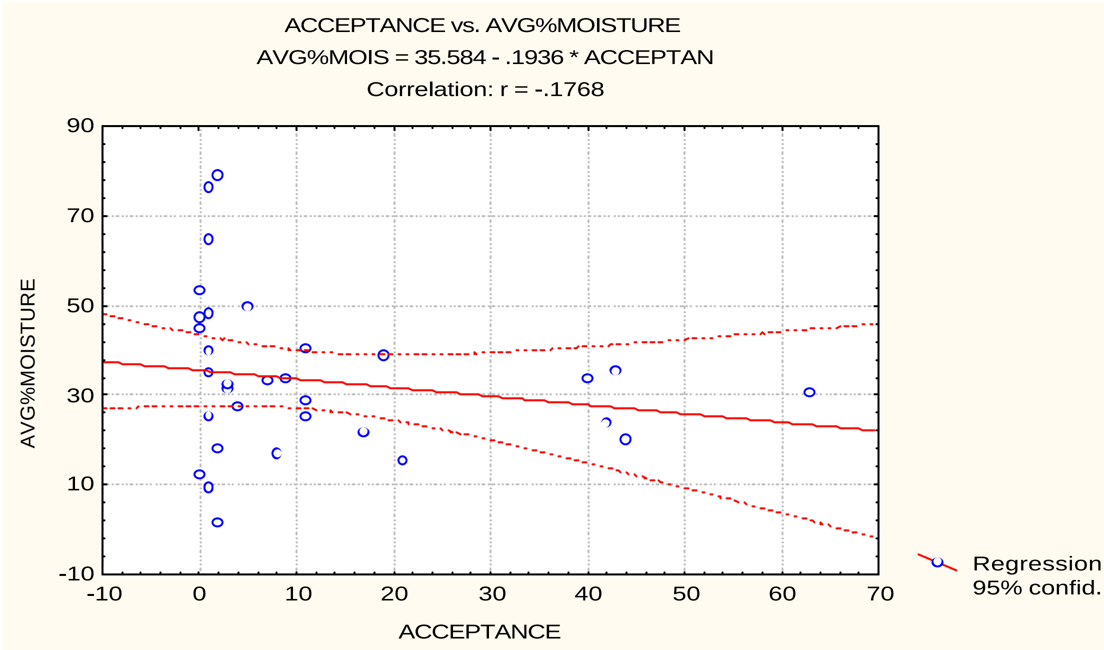


Figure 55: Grass acceptance correlation with percentage tuft moisture. An inverse relationship (r=-0.18) was computed between percent grass moisture content and "Acceptance".

5.3.3 Interactive effects (Multiple linear regression)

Multiple regression analysis was not able to highlight any interactive effects between the dependent variable "Acceptance" and the various chemical and physical independent variables or properties of the grasses in feeding patches (Table 59).

Table 59: Multiple regression summary for the dependent variable "Acceptance". All possible explanatory variables used and the amount of variability each explains.

	BETA	St. Err. of BETA	B	St. Err. of B	t(19)	p-level	Mean	St.dev.
Intercept			5.163	20.357	0.254	0.802		
P/mass	0.293	0.299	0.046	0.047	0.979	0.340	132.283	
%N	0.047	0.552	1.699	20.099	0.085	0.934	0.981	
%P	0.071	0.459	17.611	114.473	0.154	0.879	0.142	
S: L	0.017	0.274	1.466	23.542	0.062	0.951	0.441	
%Moisture	-0.189	0.371	-0.160	0.315	-0.509	0.617	32.050	

$R = 0.267$, $R^2 = 0.071$, $F(5,19) = 0.292$, $p < 0.910$, $SE = 17.397$

5.4 Summary and Conclusions

This study has shown the ability of buffalo to select for specific grass species, in order to maximise for crude protein and other minerals.

Species selection within the KNP seems consistent both spatially and temporally.

This component of the study wasn't able to show which of the grass dependent variables, or combination thereof, was important in determining acceptance. The methods employed were most likely inadequate (the use of mean values), and one would ideally need to compare these variables measured from utilised tufts with those of unutilised ones, to be able to detect any real differences.

What this portion of the study did show was the grass species that buffalo preferred and avoided. The five most preferred species were: *Panicum maximum, Themeda triandra, Panicum coloratum, Digitaria eriantha and Urochloa mosambicensis.* Acceptance of these species is highest over the dry months and lowest over the rainy season, when the variety of accepted plants increases probably due to an overall increase in palatability of the general grass sward.

Tuft phytomass showed the strongest positive linear relationship with acceptance, while surprisingly, percentage moisture content showed a negative correlation. It was surprising because a positive correlation exists between percentage moisture content and percentage leaf Nitrogen and Phosphorus content and one would expect buffalo to be maximising on these limiting nutrients over the dry months.

No interactive effects were evident in the multiple linear regression analysis, where all independent variables were investigated.

6 Chapter 6: Implications for management of buffalo populations

6.1 Introduction

Effective management of an ecosystem, a protected area or animal population can only be carried out with a comprehensive understanding of the entity being managed. Wildlife or conservation management seldom has the luxury of comprehensive understanding of the systems being managed and this study would be incomplete unless the scientific conclusions are contextualised for management. Buffalo metapopulation management in South Africa requires sound knowledge of the resource requirements of the species, which ideally should be ascertained from a wild free-ranging population, as a benchmark. Melton & Heard (1992) claim that only when an ungulate's foraging behaviour, under optimal resource conditions is known, can it serve as an index of habitat quality. Understanding these resource requirements allows management of the reserve or ranch to manage the veld (vegetative resource) in such a way as to meet these daily requirements and ensure a healthy productive population. As a member of the "Big Five" buffalo have always been a highly valued species in the hunting fraternity as well as in ecotourism operations. Their monetary value has recently increased to unprecedented levels with the advent of disease-free breeding endeavours, where common diseases to this species are outbred to allow for translocation to all regions of the country. Due to the expense involved with purchasing a disease-free herd and its re- establishment, it necessitates now more than ever, a sound knowledge of the species, its habitat preferences and physiological requirements, to reduce unnecessary mortalities and promote positive population growth.

Apart from these generic reasons for requiring sound ecological data on the species, much herbivore research in the KNP has been focussed on the browsing guild (du Toit, 2003), with detailed studies on grazers comparatively lacking. Several studies that began on buffalo in the park were never completed. Other studies investigated the micro- or macro-patch (Macandza *et al*., 2004; Wentzel *et al*., 1991) of buffalo with no consideration for intermediate patch scales.

Bovine tuberculosis (BTB, *Mycobacterium bovis*) has entrenched itself in the KNP system, particularly in the buffalo population, which is considered the primary maintenance host of the disease (Bengis *et al.*, 1996). This pathogen has no detectable deleterious effect on population structure at this stage (Rodwell *et al*., 2001; Caron *et al.*, 2003) but may have in the future, should prevalence levels of the disease increase. Buffalo are naturally regulated by environmental extremes, which depletes life-giving resources (Sinclair, 1974). Understanding these resource limitations may enable managers to predic t future impacts of the combined effects of BTB and drought on the population, and take necessary management action pre-emptively to avoid unnecessary long-term impacts.

6.2 Synthesis of research and potential management implications.

6.2.1 Managing for habitat preferences

Buffalo have several habitat requirements besides f feeding, including protection from environmental extremes, predator avoidance and water for drinking and wallowing. This study has shown how these factors contribute to the selection of feeding patches as patch independent variables. Mugangu *et al*. (1995) found the factors affecting habitat selection of buffalo herds in Virunga National Park, Zaire appeared to be food quality, proximity to water, and risk of predation; which compare well with my study's findings.

Observation revealed that herds fed in relatively open areas (herds feeding are vulnerable to lions as vigilance is low, necessitating them to use areas of good visibility) where a more heavily wooded area was within a reasonable walking distance. Once herds were finished feeding they would take cover beneath the canopy of large trees and wait out the heat of the day.

This meant that resting individuals could get up at any time and individually or in small groups (especially bulls) move back into the patch to feed intermittently. This was especially apparent in the winter months when herds would include a third feeding session into their daily routine, during midday, a similar pattern to that seen by Sinclair (1977) in Serengeti. This was due to lower daytime temperatures and lower winter quality of feed.

These variable habitat requirements can be promoted by implementing management strategies that create mosaic effects in vegetation structure, and not the agricultural approach of vegetative homogeneity. This will influence fire regimes, artificial bush clearing and the placement of water points.

6.2.2 Bulk grazers are selective feeders

A common perception in literature is that bulk feeders are not selective for forage (van Hoven, 1990) and as such only require large quantities of material, which they presumably would obtain randomly from whatever is immediately available to them. Other studies have shown that buffalo, as a ruminant, require a combination of high quality grass and high fibre content (Beekman & Prins, 1989), selecting for relatively nutritious grass species and parts in order to maximise intake of protein and carbohydrates (Sinclair, 1977).

The central fact that has emerged from this work is that whilst buffalo are certainly bulk-grazers, physiologically constrained as such by a capacious rumen chamber and the nature of their food source, they do and are capable of selecting for specific plant species. These preferred species remain in the diet of the herds throughout the year, although their dietary contribution may vary seasonally.

This information is critical when veld management decisions need to be made, as these decisions need to ensure that any management action will retain an adequate percentage of these preferred species in the grass sward.

6.2.3 Carrying capacity determination

Most carrying capacity (CC) determination methods produce a single figure that relates to the total biomass, thence the number of animals, that a given area can sustain for one year (Meissner, 1982; Mentis & Duke, 1982). No consideration is given to the specific habitat requirements of the species concerned, nor to possible facilitatory or inter-specific competition that may take place between such grazing species, in turn affecting this figure positively or negatively. As such, detail is not presently included in any CC determination method, and a manager would need to consider the habitat preferences of buffalo to make a subjective adjustment to any CC figure computed.

Vegetation communities are hierarchical in nature (Senft *et al*., 1987) with several micropatches combining to form a larger feeding patch that in turn combined forms a larger landscape, hence vegetation communities are affected by scale (Panagos, 1995; Westfall *et al*., 1996). The CC of an area for buffalo could thus be determined by using the percentage suitable feeding patches (or vegetation communities at fine scale) contained within a landscape or reserve. This may be difficult to achieve in reality, but may be possible with remote sensing images and/or intensive infield vegetation surveying. Herds not only need a critical abundance of preferred species within a patch, before they will use it, but they also have the spatial requirement of a suitably large patch or area to accommodate the entire herd. Patch size is thus likely related to herd size, as can be seen with buffalo bulls that commonly utilise narrow corridors of suitable habitat along riverine areas (Sinclair, 1974), and needs to be considered when considering patch requirements.

6.2.4 Artificial water points

Available drinking water was possibly the largest constraint on how far the herds could move in search of suitable forage. Preferring to drink twice during daylight hours, herds were restricted to areas of permanent water. The most distant patch recorded from water was 5.6km during the dry season, meaning the herd was restricted to drinking once a day due to the long distances required to travel to obtain suitable forage. This ranging distance should be considered when placing artificial water points. Water points need to be placed considering dry season water availability. Impact around waterholes in winter can be severe (an effect known as a Piosphere (Thrash, 1997)) and depending on the suite of other ungulates species coexisting with the buffalo, cognisance needs to be taken of the distance separating waterpoints. Should shy or water independent ungulate species occur on the reserve, pockets of veld remaining inaccessible to buffalo should be encouraged, meaning that distances between water points may need to approach ten kilometres. This will provide habitat for these water independent species and also ensure a move even distribution of movement over the year, as herds will then be able to use these under-utilised zones during the rainy season, when natural pools and ephemeral streams provide water and ultimately access to these areas.

6.2.5 Supplementary feeding

Grass responds rapidly to changes in soil moisture (du Toit, 2003). This effect is illustrated by these plants having peaks in crude protein content that coincide with rainfall events (Figure 56 and Figure 3). When soil moisture is high, the percentage Nitrogen and Phosphorus fixed in the grass tufts is also correspondingly high, supplying adequate nutrients and minerals to grazers over this period. During dry spells the bulk of available forage can no longer supply adequate nutrients to the grazing guild. In large reserves animals can compensate for this by utilising riverine and low-lying areas that have relatively high soil moisture content and thus retain a degree of green grass (Sinclair, 1977; Macandza *et al.*, 2004). Smaller reserves face a more difficult task than larger reserves, of ensuring that the herds survive the dry period, and the use of supplementary feed becomes necessary to reduce mortality and ensure high female fecundity. Prins (1996) proposed that buffalo need to maintain a diet of at least 7% crude protein, to ensure normal physiological processes. All the veld grasses analysed during this study dropped below this critical threshold over the dry months, highlighting the necessity for managers of more intensively managed populations to supply protein supplements over this period to ensure a healthy, productive population. Bird (2004) showed that buffalo cows had much lower calving success and calf survival over dry years than wet ones.

This effect of crude protein content dropping below a critical threshold is evident in the buffalo population of the KNP, based on aerial census data conducted annually by SANParks (Whyte, 2004). The buffalo are regulated by long-term trends in rainfall, with the KNP population approaching 30000 during good rainfall periods, and dropping to about 15000 during dry ones. These drastic fluctuations in population numbers can be avoided if adequate, nutritious forage and water is provided over dry years/ seasons. Interestingly, three of the five most preferred grass species of buffalo namely, *Panicum coloratum, Panicum maximum and Urochloa mosambicensis* also showed the highest crude protein content throughout the year, but especially over the rainy season (Appendix 4 tabulates percentage Nitrogen for all grasses sampled over the study period).

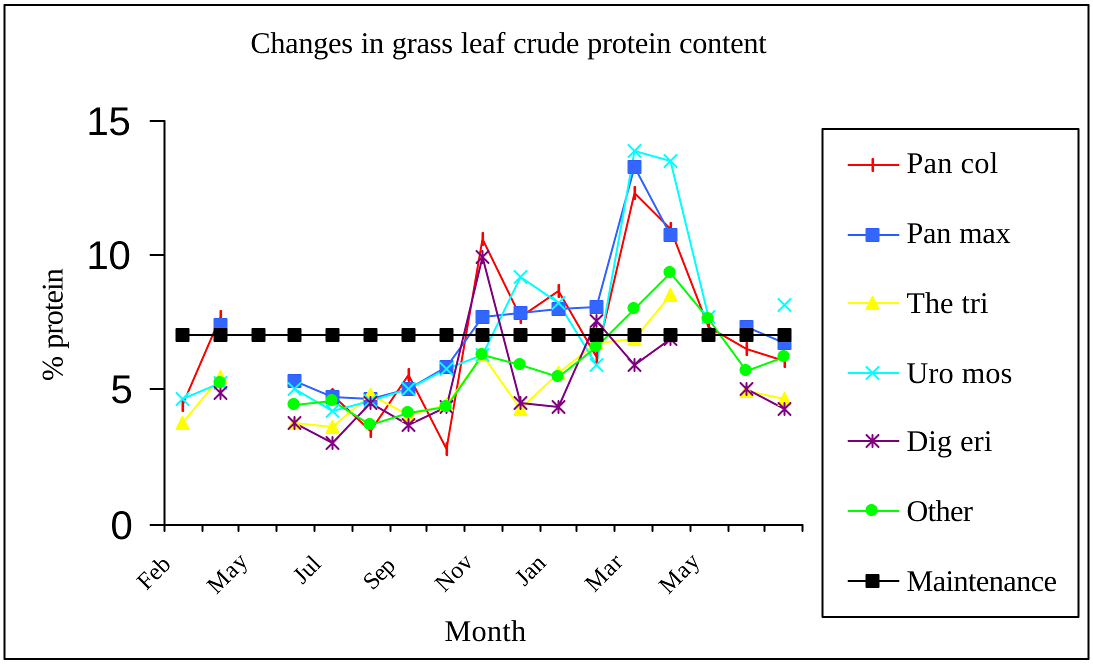


Figure 56: Comparing the crude protein content of preferred grass species over the duration of the project as well as with the other less selected species. All are compared to the 7% threshold (maintenance level) proposed by Prins (1996).

6.2.6 Fire regime

Post burn regrowth is a well sought after resource for most ungulates, with buffalo being no exception. New growth is higher in crude protein and lower in crude fibre (Field, 1976). Green flushes at the beginning of the wet season provide a high protein food source to help replenish depleted reserves suffered during the dry season. Fire is a natural and necessary component of any ecosystem and should be employed into the management of any natural area. Burn blocks need to be large enough to handle the influx of game onto the area. Buffalo too will remain in a burnt area for weeks before moving on. However, caution must be exercised over the dry season and dry cycles. While grasses are dormant over this period and any possible negative impacts on the herbaceous layer by burning will be minimal (Tainton, 1999), buffalo still require bulk forage to perform optimally, and should the bulk of a herd's home range be removed by fire over a dry spell, losses and greatly reduced performance, can be expected.

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Appendix 1

Coordinates of feeding patches and control sites. An "A" suffix depicts a control patch.

Releve	UTM_E	UTM_N
1	380048	7315479
1A	379877	7315659
2	383277	7316156
2A	383416	7315879
3	382676	7316507
3A	382845	7316564
4	382136	7316647
4A	381992	7316691
5	383478	7314603
5A	383771	7314397
6	374104	7313431
6A	374390	7313742
7	371741	7314311
7A	371565	7314215
8	372149	7314355
8A	372421	7314413
9	355472	7299552
9A	355281	7299749
10	357668	7300570
10A	357790	7300241
11	359478	7301450
11A	359481	7301725
12	379316	7311118
12A	379510	7310998
13	375016	7308960
13A	374894	7309030

Releve	UTM_E	UTM_N
44	388043	7310794
44A	387760	7310831
45	372299	7294569
45A	372502	7294606
46	380792	7318217
46A	380711	7318443
47	384911	7308115
47A	384908	7307866
48	377458	7281715
48A	377551	7281497
49	387623	7312512
49A	387329	7312492
50A	381861	7317616
50	382109	7317581
51A	381452	7316845
51	381490	7317140
52	356146	7292568
52A	356132	7292814
53A	355226	7299119
53	355121	7299333
54A	382591	7316818
54	382341	7316950
55A	361320	7300557
55	361265	7300879
56	361577	7299188
56A	361357	7299278

14	356071	7300365	57	383257	7315509
14A	356250	7300206	57A	383080	7315416
15	355024	7297793	58	387591	7315602
15A	354919	7297868	58A	387305	7315537
16	355575	7296991	59	389795	7312961
16A	355462	7297012	59A	389644	7313107
17	385445	7313359	60	383545	7316099
17A	385563	7313146	60A	383710	7315924
18	373580	7313934	61	372187	7314260
18A	373519	7313503	61A	372003	7314158
19	384153	7315507	62	372928	7313764
19A	384386	7315803	62A	372861	7313430
20	385722	7313359	63	354874	7275014
20A	385692	7313682	63A	354655	7275026
21	357468	7299741	64	357062	7273662
21A	357365	7299694	64A	356913	7273400
22	357661	7300518	65	384524	7322304
22A	357839	7300555	65A	384308	7322071
23	373665	7313395	66	361211	7299858
23A	373682	7313563	66A	361214	7299605
24	374512	7311750	67	361001	7298860
24A	374478	7311485	67A	361215	7298750
25	359395	7301220	68	370558	7309359
25A	359437	7301404	68A	370929	7309742
26	355926	7296497	69	359339	7299832
26A	355978	7296726	69A	359047	7299523
27	377253	7315101	70	370916	7309471
27A	377318	7314938	70A	370797	7309672
28	362506	7288720	71	378901	7313879
28A	362410	7288678	71A	379168	7314220
29	374453	7305407	72	359591	7298255
29A	374240	7305369	72A	359348	7298356

30	380514	7310266
30A	380450	7310006
31	355149	7296650
31A	355100	7296252
32	383937	7319381
32A	383719	7319390
33	359228	7299579
33A	359294	7299382
34	357766	7300389
34A	357890	7300501
35	379260	7310944
35A	379421	7311218
36	375589	7311926
36A	375376	7311912
37	361248	7300816
37A	361289	7300670
38	361683	7301465
38A	361470	7301588
39	388002	7315487
39A	387895	7315712
40	358217	7302079
40A	358119	7301942
41	391692	7315741
41A	392087	7315871
42	374445	7291760
42A	374328	7291885
43	361781	7298064
43A	361626	7298294

73	376405	7317079
73A	376143	7316824
74	377421	7319591
74A	377247	7319521
75	365920	7302073
75A	365893	7301856
76	366112	7301637
76A	365847	7301672
77	372674	7313566
77A	372769	7313357
78	390488	7314586
78A	390317	7314715
79	360352	7297270
79A	360168	7297144
80	384106	7315268
80A	384201	7315104
81	363046	7302268
81A	363234	7302319
82	366783	7302607
82A	366765	7302344
83	384417	7314169
83A	384478	7314390
84	382046	7316857
84A	381939	7316625
85	373019	7311014
85A	372942	7311219
86	372345	7313958
86A	371820	7313763

Appendix 2

List of grass species the degree of utilisation in the two sampled seasons. Season 1 = wet season, 2 = dry season. "No, of patches" indicates the number of patches that the species occurred in, in which it was utilised. "0" indicates the species was not utilised.

Species	Season	Degree of utilisation	No. Patches
Achyropsis leptostachya	2		0
Aristida adscensionis	1		0
Aristida adscensionis	2	Light	1
Aristida congesta subsp. *barbicollis*	1		0
Aristida congesta subsp. *barbicollis*	2	Light	1
Aristida congesta subsp. *congesta*	1		0
Aristida congesta subsp. *congesta*	2		0
Aristida sp.	1		0
Bothriochloa insculpta	1	Medium	1
Bothriochloa insculpta	2	Light	1
Bothriochloa insculpta	2	Medium	1
Bothriochloa radicans	1	Heavy	1
Bothriochloa radicans	1	Light	4
Bothriochloa radicans	1	Medium	1
Bothriochloa radicans	2	Light	3
Bothriochloa radicans	2	Medium	2
Brachiaria deflexa	1	Heavy	1
Brachiaria deflexa	1	Light	1
Brachiaria deflexa	2		0
Brachiaria eruciformis	1	Medium	1
Brachiaria nigropedata	1	Heavy	1

Brachiaria nigropedata	1	Light	1
Brachiaria nigropedata	1	Medium	1
Brachiaria nigropedata	2	Heavy	1
Cenchrus ciliaris	1	Unspecified	2
Cenchrus ciliaris	1	Heavy	3
Cenchrus ciliaris	1	Medium	2
Cenchrus ciliaris	2	Heavy	11
Cenchrus ciliaris	2	Medium	1
Chloris gayana	1		0
Chloris gayana	2	Light	1
Chloris mossambicensis	2	Heavy	1
Chloris pycnothrix	1		1
Chloris virgata	1		0
Chloris virgata	2		0
Cymbopogon excavatus	1	Heavy	1
Cymbopogon excavatus	2		0
Cymbopogon plurinodis	1	Heavy	4
Cymbopogon plurinodis	1	Light	3
Cymbopogon plurinodis	1	Medium	3
Cymbopogon plurinodis	2	Heavy	1
Cymbopogon plurinodis	2	Light	5
Cymbopogon plurinodis	2	Medium	1
Cynodon dactylon	2		0
Cyperus sp.	1	Medium	1
Cyperus sp.	2		0
Dactyloctenium aegyptium	1	Light	1
Digitaria eriantha	1	Heavy	14
Digitaria eriantha	1	Light	3
Digitaria eriantha	1	Medium	2
Digitaria eriantha	2	Heavy	12
Digitaria eriantha	2	Light	6
Digitaria eriantha	2	Medium	5

Diheteropogon amplectens	1		0
Diheteropogon amplectens	2		0
Enneapogon cenchroides	1		0
Enneapogon cenchroides	2	Light	1
Enneapogon scoparius	1	Light	1
Enneapogon scoparius	2		0
Eragrostis chloromelas	2		0
Eragrostis cilianensis	1	Light	1
Eragrostis cilianensis	2		0
Eragrostis gummiflua	1		0
Eragrostis rigidior	1		0
Eragrostis rigidior	2	Light	1
Eragrostis rigidior	2	Medium	1
Eragrostis superba	1	Heavy	1
Eragrostis superba	1	Medium	2
Eragrostis superba	2	Light	3
Eragrostis superba	2	Medium	2
Eragrostis trichophora	1		0
Fingerhuthia africana	1		0
Fingerhuthia africana	2		0
Heteropogon contortus	1	Unspecified	1
Heteropogon contortus	1	Heavy	1
Heteropogon contortus	1	Light	2
Heteropogon contortus	2	Heavy	5
Heteropogon contortus	2	Light	2
Heteropogon contortus	2	Medium	10
Ischaemum afrum	1	Heavy	1
Ischaemum afrum	1	Light	2
Ischaemum afrum	2	Heavy	3
Ischaemum afrum	2	Medium	1
Lintonia nutans	1		0
Melinis repens	1		0

Melinis repens	2	Heavy	2
Panicum coloratum	1	Unspecified	2
Panicum coloratum	1	Heavy	6
Panicum coloratum	1	Light	5
Panicum coloratum	1	Medium	7
Panicum coloratum	2	Unspecified	1
Panicum coloratum	2	Heavy	5
Panicum coloratum	2	Light	10
Panicum coloratum	2	Medium	7
Panicum deustum	1		0
Panicum maximum	1	Unspecified	4
Panicum maximum	1	Heavy	13
Panicum maximum	1	Light	5
Panicum maximum	1	Medium	8
Panicum maximum	2	Heavy	27
Panicum maximum	2	Medium	6
Perotis patens	2		0
Pogonarthria squarrosa	1		0
Pogonarthria squarrosa	2		0
Schmidtia pappophoroides	1	Medium	1
Schmidtia pappophoroides	2	Heavy	3
Schmidtia pappophoroides	2	Medium	5
Setaria incrassata	1	Light	1
Setaria incrassata	1	Heavy	3
Setaria incrassata	1	Light	2
Setaria incrassata	1	Medium	2
Setaria incrassata	2	Light	3
Setaria sp.	1		0
Sorghum versicolor	2		0
Sporobolus cunsimilis	1	Heavy	3
Sporobolus cunsimilis	1	Light	1
Sporobolus cunsimilis	2	Heavy	1

Sporobolus ioclados	1	Unspecified	4
Sporobolus ioclados	1	Light	3
Sporobolus ioclados	2	Heavy	4
Sporobolus nitens	2		0
Themeda triandra	1	Unspecified	1
Themeda triandra	1	Heavy	4
Themeda triandra	1	Light	6
Themeda triandra	1	Medium	7
Themeda triandra	2	Heavy	3
Themeda triandra	2	Light	6
Themeda triandra	2	Medium	17
Tragus berteronianus	1		0
Tricholaena monachne	1		0
Tricholaena monachne	2		0
Trichoneura grandiglumis	1		0
Unknown sp.	1	Light	1
Unknown sp.	2	Heavy	1
Urochloa mosambicensis	1	Unspecified	1
Urochloa mosambicensis	1	Heavy	6
Urochloa mosambicensis	1	Light	8
Urochloa mosambicensis	1	Medium	3
Urochloa mosambicensis	2	Heavy	5
Urochloa mosambicensis	2	Light	11
Urochloa mosambicensis	2	Medium	6
Urochloa oligotricha	1	Heavy	1
Urochloa oligotricha	2	Heavy	1
Urochloa oligotricha	2	Light	1
Urochloa panicoides	1		0

Appendix 3

Indices of selection of the various grass species found in patches.

Where:

A = Number of patches in which species occurred

B = Number of patches in which species was utilised

C = Index of selection (B/A, utilisation divided by occurrence)

D = D/86, occurrence divided by total feeding patches sampled

E = B/86, nr. of patches in which utilised divided by total feeding patches sampled.

Species	A	B	C (%)	D (%)	E (%)
Panicum maximum	69	63	91	80	73
Themeda triandra	49	44	90	57	51
Panicum coloratum	57	43	75	66	50
Digitaria eriantha	48	42	88	56	49
Urochloa mosambicensis	68	40	59	79	47
Heteropogon contortus	30	21	70	35	24
Cenchrus ciliaris	22	19	86	26	22
Cymbopogon plurinodis	22	17	77	26	20
Sporobolus ioclados	12	11	92	14	13
Setaria incrassata	26	11	42	30	13
Bothriochloa radicans	26	11	42	30	13
Schmidtia pappophoroides	18	9	50	21	10
Eragrostis superba	33	8	24	38	9
Ischaemum afrum	7	7	100	8	8
Sporobolus cunsimilis	5	5	100	6	6
Brachiaria nigropedata	5	4	80	6	5
Bothriochloa insculpta	10	3	30	12	3
Urochloa oligotricha	5	3	60	6	3
Brachiaria deflexa	6	2	33	7	2
Eragrostis rigidior	12	2	17	14	2
Melinis repens	2	2	100	2	2

Unknown sp.	2	2	100	2	2
Cymbopogon excavatus	2	1	50	2	1
Cyperus sp.	1	1	100	1	1
Chloris mossambicensis	1	1	100	1	1
Dactyloctenium aegyptium	1	1	100	1	1
Brachiaria eruciformis	1	1	100	1	1
Chloris gayana	2	1	50	2	1
Enneapogon scoparius	8	1	13	9	1
Eragrostis cilianensis	3	1	33	3	1
Chloris pycnothrix	1	1	100	1	1
Aristida congesta subsp. *barbicollis*	11	1	9	13	1
Enneapogon cenchroides	5	1	20	6	1
Aristida adscensionis	7	1	14	8	1
Fingerhuthia africana	2	0	0	2	0
Aristida congesta subsp. *congesta*	3	0	0	3	0
Eragrostis trichophora	3	0	0	3	0
Pogonarthria squarrosa	4	0	0	5	0
Panicum deustum	1	0	0	1	0
Sorghum versicolor	1	0	0	1	0
Urochloa panicoides	1	0	0	1	0
Perotis patens	1	0	0	1	0
Eragrostis look-alike	1	0	0	1	0
Chloris virgata	2	0	0	2	0

Appendix 4

Index to the full grass species names where only abbreviations have been given.

Abbreviation	Full species name	Abbreviation	Full species name
Ach lep	*Achyropsis leptostachya*	Era rig	*Eragrostis rigidior*
Ari ads	*Aristida adscensionis*	Era sup	*Eragrostis superba*
Ari bar	*Aristida congesta* subsp. *barbicollis*	Era tri	*Eragrostis trichophora*
Ari con	*Aristida congesta* subsp. *congesta*	Fin afr	*Fingerhuthia africana*
Ari sp.	*Aristida* sp.	Het con	*Heteropogon contortus*
Bot ins	*Bothriochloa insculpta*	Isc afr	*Ischaemum afrum*
Bot rad	*Bothriochloa radicans*	Lin nut	*Lintonia nutans*
Bra def	*Brachiaria deflexa*	Mel rep	*Melinis repens*
Bra eru	*Brachiaria eruciformis*	Pan col	*Panicum coloratum*
Bra nig	*Brachiaria nigropedata*	Pan deu	*Panicum deustum*
Cen cil	*Cenchrus ciliaris*	Pan max	*Panicum maximum*
Chl gay	*Chloris gayana*	Per pat	*Perotis patens*
Chl mos	*Chloris mossambicensis*	Pog squ	*Pogonarthria squarrosa*
Chl pyc	*Chloris pycnothrix*	Sch pap	*Schmidtia pappophoroides*
Chl vir	*Chloris virgata*	Set inc	*Setaria incrassata*
Cym exc	*Cymbopogon excavatus*	Set sp.	*Setaria* sp.
Cym plu	*Cymbopogon plurinodis*	Sor ver	*Sorghum versicolor*
Cyn dac	*Cynodon dactylon*	Spo cun	*Sporobolus cunsimilis*
Cyp sp.	*Cyperus* sp.	Spo ioc	*Sporobolus ioclados*
Dac aeg	*Dactyloctenium aegyptium*	Spo nit	*Sporobolus nitens*
Dig eri	*Digitaria eriantha*	The tri	*Themeda triandra*
Dih amp	*Diheteropogon amplectens*	Tra ber	*Tragus berteronianus*
Enn cen	*Enneapogon cenchroides*	Tri mon	*Tricholaena monachne*
Enn sco	*Enneapogon scoparius*	Tri gra	*Trichoneura grandiglumis*
Era chl	*Eragrostis chloromelas*	Unk sp.	*Unknown* sp.
Era cil	*Eragrostis cilianensis*	Uro mos	*Urochloa*

			mosambicensis
Era gum	*Eragrostis gummiflua*	Uro oli	*Urochloa oligotricha*
Era loo	*Eragrostis* look-alike	Uro pan	*Urochloa panicoides*

Appendix 5

Mean leaf crude protein content of grasses over study period

Species	Feb	Apr	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Ari ads		4.37	5.12													
Ari bar						3.50				6.44						
Bot ins		5.56										5.81			6.19	6.06
Bot rad		7.75	6.25		4.42	4.69	4.58	7.00		5.47	5.81	9.23	7.25	8.25	5.44	
Bra def													18.06			
Bra eru												7.75				
Bra nig				5.47							8.13					
Cen cil		5.12		5.38	3.06		6.04		8.53		5.85	12.00				5.48
Cym exc												6.19				
Cym plu		5.62	3.00			2.98	2.81		5.25	3.94		7.09	6.92		6.88	
Cyp sp.										5.94						
Dig eri		4.90	3.78	2.98	4.47	3.69	4.31	9.91	4.47	4.33	7.52	5.94	6.89		4.98	4.29
Dih amp													8.00			
Enn cen				4.25		4.31			10.37							
Enn sco		6.00														8.56
Era gum											7.69					
Era rig				5.44		3.37	4.88	7.94								
Era sup				3.38		4.07	4.59	6.19	6.06	5.44		7.00			5.12	
Era tri													7.37			
Het con		4.19		3.66	5.00	3.38	3.25		3.91			5.44			5.19	
Isc afr				4.75		7.12		3.44				8.12			5.09	
Mel rep						3.38										
Pan col	4.41	7.69		4.83	3.44	5.56	2.81	10.63	7.66	8.64	6.22	12.34	10.97	7.31	6.47	6.04
Pan max		7.40	5.30	4.73	4.66	5.06	5.81	7.72	7.83	7.97	8.08	13.25	10.78		7.31	6.70
Sch pap		3.62		4.59		4.94		8.50			6.50	10.84	8.19	6.94		6.06
Set inc			3.20	3.44	2.31	3.27		4.53	4.84	5.44	5.38	8.28				4.84
Set sp.										5.31						
Spo cun				5.77					4.06	4.63						

Spo ioc										6.75						
The tri	3.78	5.44	4.04	3.58	4.83	4.13	4.37	6.25	4.25	5.58	6.71	6.90	8.48		4.96	4.64
Uro mos	4.63	5.22	5.06	4.19	4.55	4.99	5.73	6.29	9.20	8.23	5.87	13.83	13.48	7.69		8.15
Uro oli		5.12							3.97							

Appendix 6

Mean leaf crude protein levels of grasses in feeding patches only.

Species	Feb	Apr	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Ari bar						3.50										
Bot ins												5.81			6.19	
Bot rad		8.69			4.72	5.62	4.40							8.25		
Bra def													18.06			
Bra eru												7.75				
Bra nig				5.47							8.13					
Cen cil		3.94			3.06		6.91		8.25		4.91	12.00				5.46
Cym plu		5.62	3.00			2.75	2.81		5.25	3.06		7.12	6.92		6.88	
Cyp sp.										5.94						
Dig eri		4.75	3.69	3.00	3.62	4.19	3.48	9.91	4.47	3.62	6.06	5.19	6.67		4.47	4.44
Enn sco		6.00														
Era rig				5.44		3.69	3.38	7.94								
Era sup						4.20										
Het con		4.19		3.67		3.38	3.25		4.13						5.19	
Isc afr				4.75		7.12		3.44							6.75	
Mel rep						3.38										
Pan col	5.19	6.62		4.47	3.56	5.56	2.44			8.53	5.62	13.69	9.94		7.14	6.47

Pan max		7.40	5.28	4.77	4.75	4.78	7.87	7.94	7.83	5.87	7.06	12.41	10.06		7.31	6.37
Sch pap				3.88		4.94						8.87		6.06		
Set inc			3.22			2.88		3.50	5.00	5.84		7.13				5.31
Spo cun				6.09					4.06	4.63						
Spo ioc										6.75						
The tri	4.00	5.78	4.22	3.75	5.03	4.34	5.06		4.37	5.06	7.66	6.87	8.09		4.58	4.81
Uro mos	4.63	5.66	5.06	3.94	4.59	5.05	5.62	6.75	9.50	7.67	5.87	15.08	18.00	7.63		7.65

Appendix 7

List of all plant species identified in this study.

Graminoids	Forbs
Achyropsis leptostachya	*Abutilon* sp.
Aristida adscensionis	*Agathisantheum bojeri* subsp. *bojeri*
Aristida congesta subsp. *barbicollis*	*Alsicarpus rugosus* subsp. *perennirufius*
Aristida congesta subsp. *congesta*	*Anthericum* sp.
Aristida sp.	*Asparagus* sp.
Bothriochloa insculpta	*Cephalocroton mollis*
Bothriochloa radicans	*Ceratotheca triloba*
Brachiaria deflexa	cf. *Hemizygia petrensis*
Brachiaria eruciformis	cf. *Justicia protracta*
Brachiaria nigropedata	*Cienfuegosia hildebrandtii*
Cenchrus ciliaris	*Cleome angustifolia* subsp. *petersiana*
Chloris gayana	*Cleome oxyphylla* var. *oxyphylla*
Chloris mossambicensis	*Clerodendrum ternatum* var. *ternatum*
Chloris pycnothrix	*Commelina* sp.
Chloris virgata	*Crotalaria virgulata* subsp. *grantiana*
Cymbopogon excavatus	*Cyathula lanceolata*
Cymbopogon plurinodis	*Dicoma tomentosa*
Cynodon dactylon	*Dyschoriste rogersii*
Cyperus sp.	*Heliotropicum steudneri*
Dactyloctenium aegyptium	*Hermannia boraginiflora*
Digitaria eriantha	*Hibiscus micranthus* var. *micranthus*
Diheteropogon amplectens	*Indigofera* sp.
Enneapogon cenchroides	*Ipomoea* sp.
Enneapogon scoparius	*Jatropha sp.*
Eragrostis chloromelas	*Justicia flava*
Eragrostis cilianensis	*Kohautia virgata*
Eragrostis gummiflua	*Kyphocarpa augustifolia*
Eragrostis rigidior	*Lantana rugosa*

Eragrostis superba	*Leonotis* sp.
Eragrostis trichophora	*Leucas glabrata* var. *glabrata*
Fingerhuthia africana	*Limeum pterocarpum* var. *pterocarpum*
Heteropogon contortus	*Melhania forbesii*
Ischaemum afrum	*Nidorella auriculata*
Lintonia nutans	*Ocimum canum*
Melinis repens	*Phyllanthus incurvus*
Panicum coloratum	*Rhynchosia albissima*
Panicum deustum	*Rhynchosia minima* var. cf. *prostrata*
Panicum maximum *Perotis patens*	*Sericorema sericea* *Sida alba*
Pogonarthria squarrosa	*Solanum eleagnifolium*
Schmidtia pappophoroides	*Solanum* sp.
Setaria incrassata	*Tephrosia* sp.
Setaria sp. *Sorghum versicolor*	*Tragia* sp. *Vernonia* sp.
Sporobolus cunsimilis	*Xerophyta retinervis*
Sporobolus ioclados	**Shrubs**
Sporobolus nitens	*Acacia borleae*
Themeda triandra	*Acacia exuvialis*
Tragus berteronianus	*Acacia gerrardii*
Tricholaena monachne	*Acacia nigrescens*
Trichoneura grandiglumis	*Acacia tortillis*
Urochloa mosambicensis	*Albizia harveyi*
Urochloa oligotricha	*Azima tetracantha*
Urochloa panicoides	*Balanites maughamii*
Dwarf shrubs	*Bolusanthus speciosus*
Acacia burkei	*Capparis tomentosa*
Acacia exuvialis	*Cissus cornifolia*
Acacia gerrardii	*Combretum apiculatum*
Acacia karoo	*Combretum hereroense*
Acacia nigrescens	*Combretum imberbe*

Acacia nilotica	*Combretum mossambicense*
Acacia robusta	*Combretum zeyheri*
Acacia tortillis	*Commiphora* cf. *pyraconthoides*
Acacia xanthophloea	*Commiphora* sp.
Adenium sp.	*Dalbergia melanoxylon*
Albizia harveyi	*Dichrostachys cinerea*
Albizia petersiana	*Diospyros mespiliformes*
Azima tetracantha	*Ehretia amoena*
Baby maytenus	*Euclea divinorum*
Balanites maughamii *Barleria bleferrous*	*Euclea natalensis* *Flueggea virosa*
Berchemia zeyheri	*Grewia bicolor*
Bolusanthus speciosus	*Grewia flava*
Capparis tomentosa	*Grewia hexamita*
Cassia abbreviata *Cissus cornifolia*	*Grewia monticola* *Grewia* sp.
Combretum apiculatum	*Grewia villosa*
Combretum hereroense	*Gymnosporia buxifolia*
Combretum imberbe	*Gymnosporia senegalensis*
Combretum mossambicense	*Lannea stuhlmannii*
Combretum zeyheri	*Lonchocarpus capassa*
Commiphora cf. *pyraconthoides*	*Ormocarpum trichocarpum*
Commiphora sp.	*Peltophorum africanum*
Dalbergia melanoxylon	*Sclerocarya birrea*
Dichrostachys cinerea	*Spirostachys africana*
Diospyros mespiliformes	*Strychnos spinosa*
Dombeya rotundifolia	*Terminalia prunoides*
Ehretia amoena	*Ximenia americana*
Ehretia rigida	*Ximenia caffra*
Euclea divinorum	*Ziziphus mucronata*
Euclea natalensis	**Trees**
Flueggea virosa	*Acacia gerrardii*

Gardenia volkensii	*Acacia nigrescens*
Gossypium herbaceum subsp. *africanum*	*Acacia nilotica*
Grewia bicolor	*Acacia robusta*
Grewia flava	*Acacia tortillis*
Grewia hexamita	*Albizia harveyi*
Grewia monticola	*Balanites maughamii*
Grewia villosa	*Cassia abbreviata*
Gymnosporia buxifolia	*Combretum apiculatum*
Gymnosporia senegalensis	*Combretum hereroense*
Lannea stuhlmannii *Lonchocarpus capassa*	*Combretum imberbe* *Combretum zeyheri*
Maerua parvifolia	*Dalbergia melanoxylon*
Neuracanthus africanus	*Diospyros mespiliformes*
Ormocarpum trichocarpum	*Gymnosporia buxifolia*
Ozoroa engleri *Peltophorum africanum*	*Lannea stuhlmannii* *Lonchocarpus capassa*
Rhus guenizii	*Peltophorum africanum*
Sclerocarya birrea	*Sclerocarya birrea*
Strychnos spinosa	*Terminalia prunoides*
Terminalia sericea	*Terminalia sericea*
Ximenia americana	*Ziziphus mucronata*
Ximenia caffra	
Ziziphus mucronata	

Appendix 8

Example of datasheet for collection of plant specimen samples.

Collection Sheet		
Specimen nr.	Plant name	Description

Appendix 9

Example of datasheet used for collection of floristic data of selected and control patches.

Species list						
Sample site nr:						
Spec. Nr.	Name	GF	CDC	NI	Utilised	Degree

GF Growth form

CDC Crown diameter class

NI No. of individuals in variable transect

GF Tree (single stem >2m, multi-stem >=5m)

Shrub (single <2m, multi <5m)

Dwarf shrub (woody, <1m, perennial)

Graminoid (Restios, sedges, grasses)

Forb (herbs, mainly annual)

Grass height			
1		11	
2		12	
3		13	
4		14	
5		15	
6		16	
7		17	
8		18	
9		19	
10		20	

Appendix 10

Datasheet used to collect general habitat data of selected and control patches.

Veld survey data sheet

1. Field workers name:………………………………………………

2. Date:…………………………………Time:..................……………

3. Locality

   General locality:……………………………………........…

   Herd name:…………………………………………………

   Sample site no: ……………………………………….....

   GPS…………………………………………………......

4. Environmental parameters

   Slope (in degrees)……………… Aspect (in degrees)……………….

   Geomorphological unit……………………………………..…

   Soil type (sand, loam, clay)………………………………………..

   Estimated % surface rock…………………………………..…...

5. Anthropogenic activity

   Evidence of recent fire………………………………………...

   Other disturbances……………………………………………..

   ……………………………………………………………………

6. Evidence of grazing or browsing……………………………………..

7. Mean visibility (m):N:..........E:..........S:..........W:..........Avg=................

8. Mean grass height: a. No grass ....

   b. Ankle height ....

   c. Knee ....

   d. Waist ....

   e. Shoulder ....

   f. > 1500mm ......

9. Distance to water (m) ....